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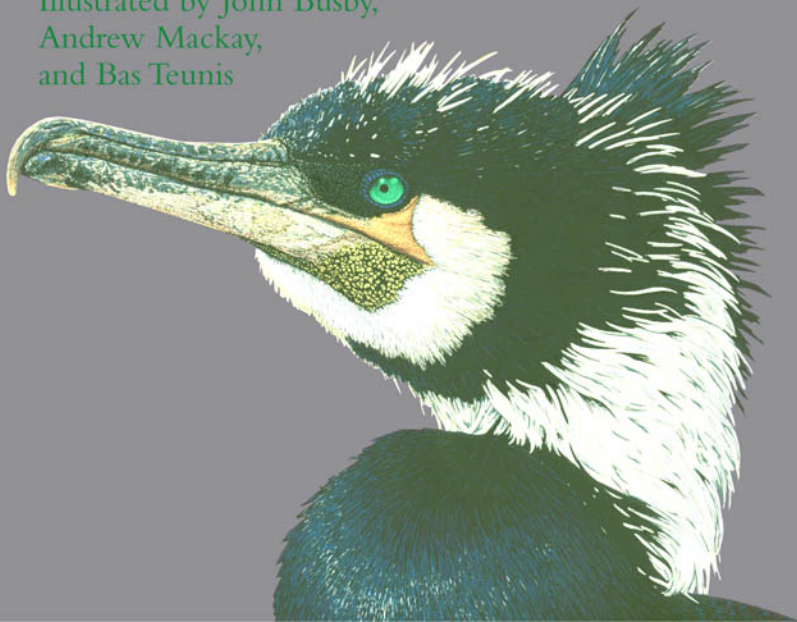


Pelicans, Cormorants, and their Relatives

The Pelecaniformes

J. Bryan Nelson

Illustrated by John Busby,
Andrew Mackay,
and Bas Teunis



Bird Families of the World

A series of authoritative, illustrated handbooks of which this is the seventeenth volume to be published

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Sulids have been **Bryan Nelson's** life-long interest. His Oxford D. Phil (1963) followed three years' work on the ecology and behaviour of gannets on the Bass Rock. Throughout 1964 the Nelsons worked alone and incommunicado on the seabirds, principally the boobies, on two of the Galapagos Islands (Galapagos: Islands of Birds 1968; Longmans-Green). Research on the endemic Abbott's booby of Australia's Christmas Island in 1967 led to several subsequent visits in the 1970s and 1980s before full protection for the island and its seabirds was achieved. In 1974 the Nelson's twins were born and he visited Aldabra under the auspices of the Royal Society of London to initiate a study of frigatebirds, later taken up by one of his Ph.D. students. In 1978 his major work 'The Sulidae: gannets and boobies' was published by (O.U.P. on behalf of Aberdeen University Press), as was his monograph on the Atlantic gannet (T. & A.D. Poyser). The influential 'Seabirds: their biology and ecology' (Hamlyn) followed in 1980. Between 1968-69 he held an IBP funded post working at Azraq in Jordan ('Azraq: Desert Oasis', Allen Lane, 1974). In 1969 he joined the Zoology Department at Aberdeen University. A sabbatical (1978/9) was spent at Cape Kidnappers (New Zealand) working on the Australasian gannet. He retired as Reader in 1982, the same year in which he was elected to the Royal Society of Edinburgh. He has been on the Board of Directors of the Scottish Seabird Centre since its inception. The Nelsons live in Galloway, Scotland. The author still visits the Bass Rock on which the gannet population has increased sixfold since the early sixties, though, alas, he cannot claim credit for that.

Andrew Mackay is a freelance artist and illustrator. He has contributed illustrations to many publications, including Birds of the Western Palearctic Concise Edition, for which he painted the seabirds and terns.

John Busby studied painting at Leeds and Edinburgh Colleges of Art and taught at ECA for 30 years until 1988. He is a member of the Royal Scottish Academy and founder member of the Society of Wildlife Artists. His passion for drawing birds grows from first-hand observation and a love of expressive line; his birds are always shown in action. His illustrations have appeared in all Dr Nelson's books including 'The Sulidae' and 'Seabirds', and over 30 other books, including 'The Penguins' in the OUP Bird Families of the World series. His own books include 'John Busby: Nature Drawings' (Arlequin), and two editions of 'Drawing Birds' (RSPB). A book of his landscape and bird paintings 'Land Marks and Sea Wings' is in preparation, (The Wildlife Art Gallery 05).

John lives in East Lothian, Scotland, a short distance from the Bass Rock, and has visited many other seabird islands around the world.

Bas Teunis studied biology at Utrecht University, The Netherlands. Since 1988, he has been working as a freelance scientific illustrator. He is best known for his work on amphibians and their behaviour, especially on the courtship of newts and salamanders. Amongst the international publications he illustrated are 'The Newts And Salamanders Of Europe' by Richard Griffiths (Poyser), and 'Amphibians And Reptiles' by Trevor Beebee and Richard Griffiths (Collins New Naturalist series). In 1994 he visited his first gannetry, and since then he has dedicated all his spare time to studying seabirds and their behaviour. In 2002 he worked for 6 months as a warden on the Farne Isles, off the Northumbrian coast. The cormorant portrait is part of a large series of seabird and coastal bird portraits in silk screen print, an ongoing project which he started in 1996.

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J. Bryan Nelson

Bird Families of the World

Pelicans, Cormorants and their relatives

*Pelecanidae, Sulidae, Phalacrocoracidae,
Anhingidae, Fregatidae, Phaethontidae*

J. Bryan Nelson

Colour Illustrations by
Andrew Mackay

Line drawings by
John Busby

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Abbreviations

ANPWS	Australian National Parks and Wildlife Service
AOS	apparently occupied site
BMR	basal metabolic rate
BP	before present
BWP	<i>Birds of the Western Palearctic</i>
DDE	Dichloro Diphenyl Dichloroethane
DDT	Dichloro Diphenyl Trichloroethane
EGI	Edward Grey Institute (Oxford)
ENSO	El Niño southern oscillation
GFA	General family account
HANZ	<i>Handbook of Australian and New Zealand Birds</i>
ICBP	International Council for Bird Preservation
IO	Indian Ocean
IUCN	International Union for the Conservation of Nature. Now 'World Conservation Union'
MYA	million years ago
PCBs	Polychlorinated Biphenyls
PO	Pacific Ocean
POBSP	Pacific Ocean Biological Survey Program
RSD	reversed sexual dimorphism
Sp Acc	Species account
USF WS	United States Fish & Wildlife Service
WeBS	Wetland Bird Survey

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General Introduction

Every seabird addresses the same basic issues and has evolved its own adaptive web. The various ways in which the pelecaniforms deal with their social requirements, such as breeding space and the relationship between partners and between parents and young, throws light on social behaviour in general. Similarly, the links between feeding/foraging and the entire complex edifice of breeding strategy in the different pelecaniforms is relevant to those same issues in other seabirds. Combining the general and the particular in this book has been complicated by the need to deal with six variably divergent families, two of which (tropicbirds and frigatebirds) are very different from the remainder and may not even belong within the *Pelecaniformes*.

For these reasons I have adopted a three-tier approach. First, the four thematic chapters encompass topics relevant to all six families:

1. Relationships within the Order.
2. Breeding behaviour, covering topics such as territorial behaviour and pair interactions from a broadly comparative viewpoint within the Order.
3. Breeding ecology, dealing with some general topics such as colonial breeding, the several components of the breeding cycle and breeding success.
4. Pelecaniforms and man, including some current conservation problems.

The second tier comprises general accounts of each of the six families, summarizing various aspects and comparing species within each. Thus, for example, flight, most behaviour, moult and

much else can be described here and omitted from the individual species accounts.

The third tier, the accounts of the 65 species within the *Pelecaniformes*, provides details such as identification, measurements and species-specific behaviour and ecology. The General Family and Species Accounts are structured so as to facilitate cross-reference. The species accounts vary greatly in detail, since there is enormous disparity in available information. For some species even basics are lacking whereas for others, special studies have provided extensive material, often of wide application and considerable explanatory value. This applies, for example, to the American white and brown pelicans, Atlantic gannet, Abbott's booby, European shag, great and double-crested cormorants and several more. Rather than reducing species coverage to a single tight formula, too much for some, far too restrictive for others, it is better to let each species illuminate where it can. For example, the world population and associated biology of the Atlantic gannet is probably better known than that of any other reasonably abundant seabird; the various aspects of clutch size and broods have been best studied in some shags; brood reduction in boobies has received special attention; spatial aspects of distribution within colonies of great and lesser frigatebirds has produced new ideas; population control has been rigorously applied to a population of double-crested cormorants and so on.

This requires space, and some readers will disagree with my priorities. I have tried both to address some general aspects of seabird biology and to provide detail in selected areas whilst ignoring other specialist topics such as parasites, vascular and

2 General Introduction

skeletal systems, most physiology and complex energetics. I wanted to give the reader a 'feel' for the pelecaniforms but it has proved difficult to make the book readable, yet at the same time rigorous and reasonably complete. I have tried to

interpret pelecaniform breeding biology, particularly behaviour and ecology, based on acquaintance with all the families except the pelicans themselves and extensive field experience of many. Ideally, each family requires its own volume.

PART I

General chapters

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Relationships

Introduction

'To regard nomenclature as more than a means to an end is pedantry and to take a minority course in a matter of convention is merely a nuisance.' (Thomson 1964)

'To be confronted with an avian humerus nearly two feet long and distinguish it by a name that means simply "Miocene Seabird" requires an unenviable dullness of spirit.' (Olson 1985a on the name *Pelagornis miocaenus*)

In this volume, the order *Pelecaniformes* comprises six families and 65 species dealt with in the following sequence: seven pelicans, nine sulids (gannets and boobies), 39¹ cormorants (cormorants and shags), two anhingids (anhinga and darter, also called snakebirds), five frigatebirds and three tropicbirds. The *Pelecaniformes* or *Steganopodes* as they were called, have seemed a natural monophyletic assemblage to many systematists, as it did to T.H. Huxley (1867) who called them the *Dysporomorphae*. But others, using evidence from the skeleton, including fossils, and from muscles, feather tracts, gut-morphology, carotid artery features, parasites, behaviour, DNA and egg-white proteins, differ about relationships within the Order and about the relationship of the peleaniforms to other major groupings. Perhaps the Order will be disbanded quite soon.

Among the 'core' families, the sulids, cormorants and anhingids are closely related to each other and less closely to the pelicans. This agrees with comparative behaviour and other evidence (for references to osteological and morphological work see Sibley and Ahlquist 1972; Hedges and Sibley 1994). The frigatebirds and tropicbirds, however, pose large

questions concerning their relationships and the Order *Pelecaniformes* may well be polyphyletic (derived from more than one ancestral line). In recognition of this, the only groups sometimes given their own sub-Order within the *Pelecaniformes* are the tropicbirds and frigatebirds. The remainder fall within the sub-Order *Pelecani*.

Each family is more or less 'good', consisting at most of different genera and usually only of species. Some accounts place the anhingas and darters with the cormorants and shags within the family Phalacrocoracidae. Indeed, the relationships within this family have spawned several confusing taxonomies.

There are nine sulids. Although authors differ in using the genus *Morus* for three gannets and *Sula* for five boobies, rather than just *Sula* for both, the osteological evidence for differentiating the two goes back to the Miocene. And now a third genus *Papasula* has been erected for Abbott's booby.

The pelicans comprise seven species, the frigatebirds five and the tropicbirds three, each within a single genus.

Broad relationships

Anatomy common to all includes: foot webbed between all four toes, the hallux, which is lower and turned forwards, being connected to the inner toe; lack of a brood patch (despite statements to the contrary concerning frigatebirds and tropicbirds in several major works); salt gland enclosed completely within the orbit whereas in most seabirds it lies in a cavity on top of the skull. The naked gular skin

6 Pelicans, Cormorants and their relatives

forming a pouch is lacking only in tropicbirds—a feature which has important consequences for its breeding biology in that it generally requires a hole or shaded site which can lead to severe competition with concomitant territorial fighting and eviction of chicks.

The external nostrils are closed (pelicans, sulids, frigatebirds), nearly closed (cormorants, anhingids) or slit-like (tropicbirds). In all other characters used to determine relationships pelecaniforms vary considerably. Relationships have been postulated between at least some pelecaniforms (usually frigatebirds and/or tropicbirds) and a formidable list of avian groups including the *Ciconiiformes* (storks, herons, spoonbills and ibises), *Falconiformes* (hawks, eagles, vultures), *Procellariiformes* (albatrosses, petrels, shearwaters), *Anseriiformes* (ducks, geese, swans), Spheniscidae (penguins), Gaviidae (divers) and Laridae (gulls, skuas and terns). An extreme view was that of Pycraft (1907) who suggested that the *Pelecaniformes* could be the ancestral stock for a plethora of other groups including penguins, tubenoses, storks and their allies and ducks, geese and swans; but this was based on skeletal evidence which, as in the case of the once-trusted palate structure, has its limitations, for instance with regard to possible convergence. The most basic evidence, that of protein structure, is sometimes incongruent with skeletal evidence (e.g. Sibley 1970; Sibley and Ahlquist 1972; Voous 1980; Warheit 1990; Friesen and Anderson 1997).

On the evidence of egg-white proteins, cormorants and sulids are especially closely related. This is supported by the pattern of their preen-wax constituents (but pelicans are different) (Jacob *et al.* 1997). The highly ritualized sexual advertising display of cormorants and sulids show close similarities (GFA). Indeed, it is astonishing that over the immense period that these two families have been separate such an improbable combination of movements has persisted in both lines. Pelicans are not as closely related to cormorants and sulids as these are to each other, a conclusion emphatically supported by behaviour. However, the pattern of egg-white proteins in the pelicans resembles that in the Atlantic gannet (Sibley 1970). DNA evidence suggests pelicans (along with the shoebill (*Balaeniceps rex*, an

aberrant heron) may be more closely related to New World vultures and storks than to sulids and cormorants (Sibley and Ahlquist 1990; Hedges and Sibley 1994).

Superficially, behavioural evidence may seem less dependable than physical characters. However, behaviour can be extremely conservative though confusion with convergent evolution is always possible even if unlikely with such complex, ritualized displays. Behaviour is most convincing when used to study relationships between families and smaller taxa, but Van Tets (1965) used the presence of a mutual face-to-face display between pair-members to suggest a relationship between procellariiforms, ciconiforms and pelecaniforms; other seabirds do not display in this way. Recently, Kennedy *et al.* (1996) subjected Van Tets's survey of pelecaniforms, especially 'hop, step and gape', to sophisticated scrutiny and showed that the behavioural data were more similar to the morphological and genetic trees than would be expected by chance.

Frigatebirds and tropicbirds emerge as comparatively distantly related to the rest of the Order. Indeed, Mivart (1878) could not find good skull characters linking the two groups. Shufeldt (1888) noted skeletal similarities between tropicbirds and shearwaters and possibly between tropicbirds and gulls; a link suggested on the quite different grounds of feather characteristics by Chandler (1916), who went so far as to say that tropicbirds were aberrant larids; an idea later reflected in Howell's (1978) analysis of the skeletal resemblances between tropicbirds and terns, though he does not suggest common descent. Shufeldt linked frigatebird skulls to those of albatrosses, as, later, did Simonetta (1963).

Opinions differ about the relationship between tropicbirds and frigatebirds. Stejneger (1885) thought they were as different from each other as each was from the core group, whilst Shufeldt thought they were closer to each other than to any of the core families. Simonetta considered tropicbirds to be an isolated genus of uncertain affinities, and Mayr and Amadon (1951) classified them as less closely related to core pelecaniforms than frigatebirds are, thus making them the most aberrant of all pelecaniforms. Indeed, Wetmore (1960) gave tropicbirds and frigatebirds, separately, sub-Ordinal rank. DNA

hybridization indicates that frigatebirds are closest to penguins, loons and the Procellariodea (Hedges and Sibley 1994). Del Hoyo *et al.* (1992) put tropicbirds in the sub-Order *Phaethontes*. One might have concluded that, at least, tropicbirds were conclusively separable from the rest of the *Pelecaniformes* but Sibley (1960) found their egg-white proteins similar to frigatebirds' but different from the others. He wrote that 'one may safely assume that the similarity between *Phaethon* and *Fregata* is the result of relationship' but 'it would be rash to ascribe the tropicbird-gull similarities to the same cause (that is, relationship) without further tests of protein identity'.

Electron microscopic examination of eggshell structure supports peleciforms as a natural group; all families except the tropicbirds show complete similarity (Mikhailov 1995). This author asserts that the shoebill is an aberrant peleciform and that it and the Ardeidae (herons)—but not the Ciconiidae (storks)—should (with the peleciforms, apart from the tropicbirds) form a single large group.

The feather-lice of tropicbirds and frigatebirds are most like those of procellariforms (Timmerman 1965); he concluded that tropicbirds, frigatebirds and tubenoses are related, but that procellariforms and other peleciforms are not.

Fossil peleciforms

Fossil birds, chiefly bone (which may have become mineralized so that it resembles stone) have been preserved in geological deposits which can now be reliably dated back to the late Jurassic (150 m years ago—MYA) though most remains are much younger. Interpretation of specimens, which are usually worn and incomplete, is specialized—almost an art—but vital to understanding present-day relationships.

Fossil evidence is included under each family, but there are general points to be made. Olson (1985a) questions the inclusion within the *Pelecaniformes* of the fossil families Eloppterigidae and Cladornithidae although he concedes that *Eostega*, which apparently had a mandible intermediate between a sulid and a cormorant, could be a peleciform. However,

Howard (1950) felt that *Eolopteryx* and *Eostega* were perhaps ancestral to the Sulidae and Phalacrocoracidae, whilst Brodkorb (1963) agreed in recognizing *Eolopteryx* and *Eostega* as sulids.

The Pelagornithidae (synonyms Dontoptyrigidae, Cyphornithidae, Pseudontornithidae and Dasornithidae) is a single family embracing various pseudodontorns (fossil forms). A jaw fragment has been found in the Upper Paleocene (65–60 MYA) of southern Kazakhstan though most fossil species appear in the early Eocene (53–48 MYA). At some point in that epoch they were probably distributed worldwide and have been found from British Colombia to Antarctica and from England to New Zealand. They were gigantic, light-boned (even lighter bones than current frigatebirds), gliding seabirds with a wing-span possibly up to 20 feet (6 m) and huge bills adorned with toothlike projections. Probably they fed by surface-dipping (Olson 1985a). Not all the many families into which, previously, pseudodontorn fragments have been placed lie within the *Pelecaniformes* but some probably do. The group is still in need of revision (Olson 1985a) and, for now, the one family (Pelagornithidae) could be acceptable. Olson remarks that one goal of any re-assessment should be to consider the possibility that peleciforms and procellariforms derive from a close common ancestor. Although the Pelagornithidae appear to show some procellariform characters, their salt glands, like the peleciforms but unlike most seabirds, lie completely within the orbit.

The plotopterids are a family of fossil peleciforms proposed by Howard (1969) on the basis of a humeral coracoid from the early Miocene (23–15 MYA) of California, and endorsed by Olson (1980). More recently Olson (1996) examined previously known material and described considerable radiation of genera and species, one of which (*Copepteryx titan*) was probably larger than any known diving bird, living or fossil. Plotopterids are related to anhingids and cormorants but with convergent similarities to penguins. They were flightless with highly specialized wings used for underwater propulsion. The sternum clearly resembled that of a peleciform. The single skull found so far resembles a gannet's but the top of the bill is missing. At least four

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species have been found in Japan, one an almost complete specimen on Ainosshima Island. The largest pterosaur was the northern-hemisphere equivalent of the giant penguin and presumably filled an equivalent niche. Both forms had apparently died out by mid-Miocene (15–10 MYA) and Olson (1985) conjectures that the massive diversification of seals and porpoises around that time provided superior competition. Warheit and Lindberg (1988) suggest that the negative correlation between seabird and pinniped diversity from 16 MYA to the present time (see also Emslie and Morgan 1994, Table 1) could be explained by competition for space or food. There is anecdotal evidence that Brandt's cormorant is excluded from some islands by sealions.

The following paragraph attempts to place the occurrence (though not the relationships) of the fossil pelecypods on a time scale. The oldest (52–38 MYA) were either pelagornithids or pterosaurs (see Warheit 1992). At around 50 MYA one finds the earliest fossil ancestors of frigatebirds and tropicbirds. The oldest 'possible' pelican dates back to around 40 MYA. It is difficult to say when the ancestral sulid/cormorant line diverged from the ancestral pelican, but sulids and cormorants themselves split around 42 MYA at which time the earliest undisputed fossils occur. Anhingids separated from cormorants at least 30 MYA but probably long before that (the earliest fossil referable to the Anhingidae was thought to be late Eocene, though it may be younger; Olson 1985a). Olson says 'almost certainly the Anhingidae, Pterosauridae and Phalacrocoracidae have a close common ancestry'. Within the Sulidae, the difference between *Morus* and *Sula* is apparent at least as far back as 15–10 MYA (Olson 1985a). The earliest pelecypods thus once coexisted with more primitive taxa such as the pseudodontornis.

Fossils of extant seabird taxa, including pelecypods, come from around 18–13 MYA at which time *Osteodontornis* (a pseudodontornis) was still widespread and small pterosaurs, about cormorant size, still extant. It appears that sulids and procellariids dominated, and it was during this period that the initial radiation of extant members of these families occurred in the North Pacific. As long ago as 13–8 MYA conditions in the area of the eastern North

Pacific from which these fossil assemblages came are thought to have been similar to those of today. Sulids prospered and though the composition of the assemblage changed considerably, the total diversity remained much the same. Indeed, there was a wider range in morphology than during the previous period. For example, *Morus* (*Miosula*) *media* had wing and leg structures similar to cormorants' whereas *Morus* (*Paleosula*) *stocktoni* more resembled wing-propelled divers. During this period the cormorants showed initial radiation.

Then between 6 or 7 and 4 MYA there was a reduction in the diversity of pelecypods. Sulids declined from extreme diversity and abundance (e.g. Warheit 1992) to one species and cormorants disappeared from the record. And, for the first time since its appearance in the fossil record, *Osteodontornis* is absent. The pseudodontornis, apparently, became extinct in the eastern North Pacific at this time, though still present in Japan and remaining into the Pliocene (5.5–1.5 MYA) in both the South Pacific and the North Atlantic. According to Warheit this decrease in seabird diversity is associated with a drop in sea level, a broad, offshore California current, and frequent though short-lived incursions of warm water presumably comparable to present-day El Niño southern oscillations (ENSOs). After the emergence of the Panamanian land bridge there was a more fluctuating marine environment than in the stable cold-water regime of the Pliocene. This may have contributed to the extinction of some taxa. Concomitantly, several molluscan taxa became extinct, suggesting an interruption in the productivity of the eastern Pacific. Nevertheless, auks increased their diversity at this time and sampling artefacts may invalidate the above hypothesis.

From 3–1.5 MYA cormorant and sulid species increased in numbers and the genus *Sula* became as diverse as *Morus*. Relating such changes in diversity to ancient climatic and geological events is obviously speculative but there is circumstantial evidence that, in cold waters, foot or wing-propelled diving is more effective than plunging, possibly because prey tends to be deeper. At any rate, 40–80 per cent of seabirds nesting in polar and sub-polar regions use feet or wings for underwater propulsion (Ainley 1977). Now, at the time at which

sulids became morphologically more diverse, presumably expanding their foraging behaviour from plunging to wing-or-foot-propelled diving, the food-producing Californian upwelling was probably strong. Conversely, the decrease in seabird diversity 7–4 MYA is associated with different conditions that may have interrupted the basic productivity of the eastern Pacific.

Taking the extant pelecaniform families in turn, the earliest records are as follows. The oldest possible ‘pelican’ is based on a femur from the late Eocene (*c.* 40 MYA), Paris Basin, and named *Protopelicanus cuvieri* Reichenbach 1853. Brunet (1970) considered it a typical pelican, somewhat more specialized than living species, but Harrison (1979) thought the femur more like that of a sulid and Olson (1985a) thought ‘it was probably not a pelican’ though it was a pelecaniform. He hints that it may have been as much like a pelagornid femur as a sulid’s. *Pelecanus halieus* is known from the late Pliocene (2–3 MYA) of Idaho. The oldest undisputed pelican came from the early Miocene (20 MYA) of France.

The Sulidae is the most primitive family of the sub-Order Peleacani (Olson 1977). The oldest possible ‘sulid’ relates to the early Oligocene (*c.* 30 MYA), though Harrison (1975) places this fossil in the Phalacrocoracidae. Sulids were abundant in the Oligocene (38–22 MYA), Miocene (24–5.5 MYA) and Pliocene. Although there are fossils from the North Pacific, no sulids presently occur there.

The oldest possible ‘cormorant’ was the related ptopterid mentioned earlier. Undisputed cormorants have been found in the Miocene.

The earliest frigate fossil comes from the early Eocene (53–38 MYA) and is probably ancestral to modern Fregata (Olson 1977).

The earliest possible ‘tropicbird’ *Prophaethon shrubsolei* Andrews 1899 is from early Eocene London clay (see Fossil tropicbirds). The earliest undisputed tropicbird comes from the mid-Miocene.

Coming to the recent past, Steadman (1989) has demonstrated the extinction of seabirds, including pelecaniforms, on a massive scale in Polynesia due to human predation: ‘nearly all species of seabirds that have survived no longer occur on most of the islands that once made up their natural range.

Fossils from archaeological sites have extended the ranges of many extant species by hundreds or thousands of km’.

Relationships within families

Pelicans

The four ‘big’ ones (great white, American white, Australian and Dalmatian) are ground nesters and considered to be replacement species in four widely separated regions, though great white and Dalmatian overlap. Their ecology and behaviour show many similarities. Spot-billed, pink-backed and brown are wholly or partly arboreal and differ far more from each other than do the ‘big’ four.

Names have given rise to some confusion about relationships. The spot-billed *Pelecanus philippensis* is the same as *P. roseus*; it occurs in the Philippines. Despite this resolution the name *P. roseus* ‘has continued to cause confusion, latterly with another species. It has been claimed as a smaller, pinker sub-species of the great white pelican or, at times, even a full species in parts of Africa and Asia’ (del Hoyo *et al.* 1992). Recent studies invalidate this by showing that size is variable within the great white and that the pink tinge is produced by a secretion of the preen gland.

Fossil pelicans

The oldest undisputed pelican is *Pelecanus gracilis* Milne-Edwards, from the Lower Miocene of France. *P. intermedius* Fraas, from the mid-Miocene of Germany, is a fairly abundant fossil, whilst a small pelican from South Australia, *P. tirarensis* Miller 1966, is also reckoned to be Miocene. Rich and Van Tets (1981) named a (new) small pelican from Australia. Pliocene fossils are more numerous. Two early species have been described from India and others from the Ukraine and (a very large fossil) from North Carolina. Late Pliocene pelicans have been found in Idaho and Florida (Emslie and Morgan 1994). Emslie (1995b) describes fossil pelicans of the extant species *P. erythrorhynchus*, from Florida. Previously, it had been recorded from late Pleistocene localities in California, Nevada and

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Kansas. Recently Olson (1999) has described a new species (*P. schreiberi*) from the lower Pliocene of North Carolina. Apparently it represents a line with no living descendants. Coming to more recent times, there are plenty of sub-fossil pelican bones of extant species in Neolithic deposits, presumably from pelicans killed for food.

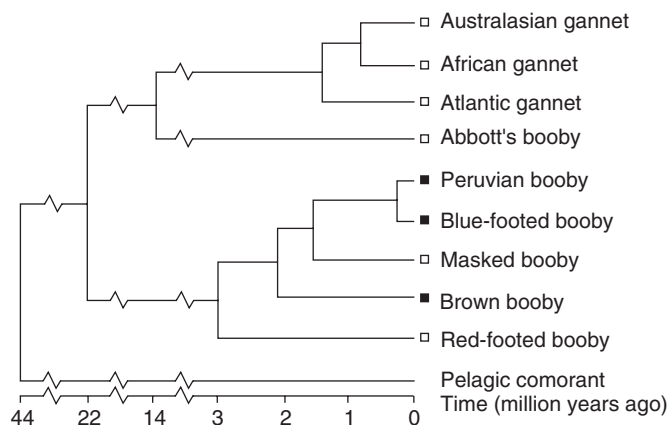
Gannets/boobies

Behavioural, molecular and osteological evidence is usually in agreement in establishing relationships within the Sulidae. Egg-white proteins are apparently quite uniform and resemble those of cormorants (Sibley and Ahlquist 1972).

Discussion of sulid intra-familial relationships has benefited greatly from recent studies by Warheit (1990, 1992) and Friesen and Anderson (1997). The question of whether sulids should be split into gannets (*Morus* sp) and boobies (*Sula* sp) formerly divided authors about evenly, but now seems resolved. The Sulidae comprises three genera: *Sula*—all extant boobies except Abbott's; *Papasula*—just Abbott's; *Morus*—the three gannets. Van Tets *et al.* (1988) described skeletal differences between *Morus* and *Sula* in every major feature examined, and Olson (1985a) noted that differences between these two taxa can be discerned at least as far back as the mid-Miocene. Warheit studied relationships within the Sulidae using 124 skeletal characters and

concluded that Recent gannets and Recent boobies are each monophyletic and that Abbott's booby is more closely related to *Sula* than to *Morus*, a conclusion opposite to that reached on a different type of evidence by Friesen and Anderson (see below). Olson and Warheit (1988) proposed *Papasula* as the new generic name for Abbott's booby, and Steadman *et al.* (1988) also conclude, as did Nelson (1978b), that *Papasula abbotti* was distinct, saying that osteologically it was no more similar to *Sula* than to *Morus*. It differs from *Sula* and *Morus* in the character of its vertebrae. Unlike the other boobies, Abbott's booby and the gannets have long humeri, possibly suggesting a closer relationship between them than between the rest of the boobies and Abbott's. Finally, Friesen and Anderson (1997), using a molecular test, concluded that gannets and boobies are separate lines, and they also group the gannet and Abbott's lines (Figure 1.1). They briefly mention behavioural evidence suggesting a link between gannets and Abbott's but omit the most striking resemblance; alone among sulids, gannets and Abbott's have a face-to-face, prolonged greeting ceremony involving loud calling and use of outspread wings.

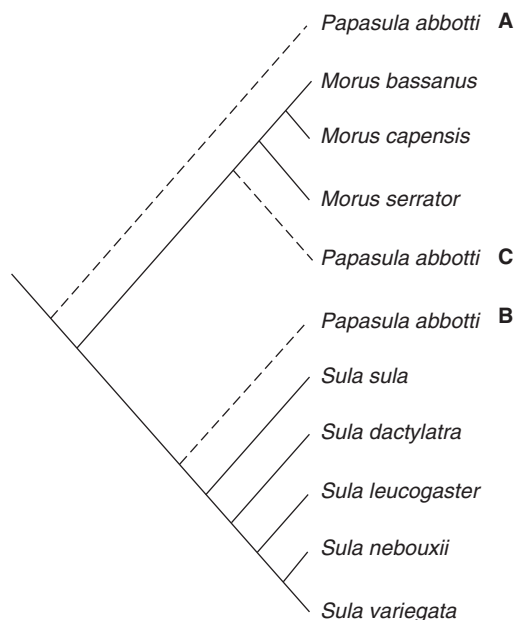
In a major evolutionary divergence, cormorants and sulids are suggested to have split around 42 MYA (see below). Within the Sulidae, molecular data indicate that the gannets/Abbott's line and the ancestral booby line diverged around 23 MYA. The gannets/Abbott's line then split, to give the



1.1 Evolutionary relationships within the Sulidae. (From Birt-Friesen and Anderson 1997.)

ancestors of present-day gannets and Abbott's booby, approximately 14 MYA. The extant lineages of the boobies (other than Abbott's) and of the gannets arose comparatively recently, the former within the last 3 MY.

For the boobies (excluding Abbott's), Warheit used numerical cladistic methods in his study of skeletal features and his relationships, summarized in Figure 1.2, are (like those of Friesen and Anderson (1997), similar to mine (Nelson 1978b) except for the relative positions of the masked and brown boobies. The blue-foot and Peruvian are recognized as sister species which may have diverged only since the last interglacial and Warheit (like Friesen and Anderson) makes them a monophyletic group with the masked booby. Unlike Friesen and Anderson, though, he makes the brown booby sister taxon to the red-foot. One can readily see the behavioural similarity between masked, blue-footed and Peruvian boobies, particularly in their shared, highly distinctive territorial display (see Figure 5.14). The red-foot is the most divergent and my comparative behaviour study (Nelson 1978b) concurs.



1.2 Modification of Nelson's phylogeny of the Sulidae showing three hypotheses. Dashed lines represent three alternative relationships for *Papasula abbotti*. (From Warheit 1990.)

Warheit could not resolve the relationships between the three modern gannets. Friesen and Anderson make the African and Australasian gannets closer relatives than either is to the Atlantic—a fairly obvious conclusion which I reached by comparing their morphology, ecology and behaviour (Nelson 1978b). African and Australasian gannets will form mixed pairs in the wild, both in Africa and Australia, though it is highly unlikely that either could do so with the Atlantic gannet. Yet the close relationship between all three gannets cannot be doubted. Both their special relationship and their differences could be met by giving all three the status of allo-species, which together form a super-species (*sensu* Amadon 1966).

Friesen and Anderson's (1997) analysis is of the utmost interest in untangling the situation. Their phylogenetic tree, derived from cytochrome b sequences, suggests that the three lineages of gannets did not arise simultaneously: . . .

. . . but 2 MYA, during the climatic oscillations of the Pliocene, the ancestral gannet appears to have split into northern and southern lineages. This was accompanied or followed by adaptation to different oceanographic regimes (Nelson 1978b). Approximately 0.6 MYA, possibly during the Kansan glacial period, the southern lineage diverged into African and Australasian populations. This scenario contrasts with that of Nelson (1978b) who proposed that the Cape gannet arose from the Australasian and the northern gannet [Atlantic gannet] was derived from the Cape gannet.

Their conclusion, accommodating as it does the special Australo-African relationship and emphasizing the difference between these and the Atlantic gannet, seems preferable. Data on lice (R. Palma, personal communication) support the splitting of gannets into three taxa, though he considers sub-specific rank to be adequate.

On the matter of common names, I consider it inappropriate to call the Atlantic gannet the 'Northern' gannet. 'Atlantic' is geographically more

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precise and consistent with 'African' and 'Australasian', each of which refers to a discrete geographical location. Since African gannets also occur in the Atlantic one could use the name 'North Atlantic gannet' rather than simply 'Northern', since 'Northern' could be the north Pacific. But Atlantic gannet seems a reasonable contraction, unlikely to cause confusion.

Warheit (1990) looked in detail at the wings and shoulder girdles of sulids with (in the Recent sulids) particular reference to their habit of diving and using their wings to swim underwater. This revived an old debate. The relative lengths of the upper and lower arms has been much used as an indicator of sulid taxonomy. When the upper is longer than the forearm it imparts a distinctive profile to the wing and affects both flight and use of the wing as an underwater propellant. Bourne (1976) considered that fossil sulids from the Miocene of California (*Morus media* and *M. stocktoni*), which had long upper arms and short forearms, were adapted for gliding and for manoeuvrability underwater, where a large distal segment of the wing would be a disadvantage. He noted that the present-day boobies (except Abbott's) have short upper-arms and long forearms, which imparts greater manoeuvrability in air, whilst gannets, and to a lesser extent Abbott's booby, have long upper-arms which increases gliding ability, and short forearms which are an advantage in deep-diving and (Warheit suggests) underwater flight. Nevertheless, he comments, the aerofoils of gannets and boobies do not differ appreciably in aerodynamic properties and indeed both groups are plunge-divers. In addition to the major arm bones, the length of the 'hand' (manus) of the wing is also variable in the sulids, differing significantly between the Recent gannets and boobies, with the former showing the relatively longer hand. The hand is extremely short in *Papasula abbotti*, which is more like *Morus* in the relative length of its humerus; but *Papasula* more resembles *Sula* in the relative lengths of its forearm and wing-phalanx. Also, *Papasula* has an extremely short carpometacarpus. Nevertheless, overall it is the length of the humerus relative to other wing bones that plays the largest part in differentiating Recent *Morus* from Recent *Sula*.

Wings evolve in harmony with the pectoral girdle and body size, and Warheit (1990) duly weighted these elements. Although gannets are larger than boobies, the size of their wings relative to body size is at most only equal to that of the boobies. The Peruvian booby differs significantly from its sister species (blue-footed and masked) in having a relatively long coracoid and short humerus and ulna, the latter bone being shorter than in any other sulid. In respect of its short ulna it does resemble the gannets, but in its short humerus it does not.

This sheds little light on the adaptive value of the differences. Probably the gannets, especially the Atlantic, dive from the greatest height and penetrate most deeply, followed by the masked booby; and the red-footed booby, especially, hunts on the wing, picking up prey in the air or plunging more shallowly (personal observation). Both *Morus* and *Sula* species, for example Atlantic gannets, brown and Peruvian boobies (and probably others) use their wings below the surface. Warheit comments that gannets and Peruvian boobies also have the shortest wings, but what of the other boobies that use them underwater? Wing length *per se* is not necessarily the most functionally significant feature. It is the relative proportions of the components and associated structures (sternum, coracoid and scapula) that give the wing its functional significance for flight in the air and underwater. For example, the gannets, the Peruvian booby, and to a lesser extent the brown booby all have relatively long ulnas but very different humeri. Thus, each of them have short wings—the gannet's because the ulnas are short though the humeri are long and the boobies because, in particular, the humeri are short. The Peruvian booby has a shorter wing in relation to body size than the masked or blue-footed booby but the relative proportions of the wing elements are the same. Warheit notes that although in wing-length relative to body-size the Peruvian is more like the gannets than the other boobies, it nevertheless maintains 'proper' booby proportions (short humerus); it is the gannets that have departed from the basic sulid ground-plan.

Finally, Warheit (1990) notes that any particular set of adaptive characters, here those that have produced wing-propelled diving in sulids, can evolve

only under the constraints of the remainder of the characters that make up a sulid.

‘Although the morphology of the gannet wing may be the optimal solution for wing-propelled diving in the Sulidae, it may not be the optimal solution for wing-propelled diving in itself. ‘Sulidness’ (history and ecology) may constrain gannets from evolving a more efficient wing-propelled diving morphology’

I would add that an important factor in this constraint has been the selection pressures favouring the evolution of wings for fast, far flight, to facilitate optimal use of resources during breeding. This equation will differ between sulid species, and with it the wing-body morphology. It is the same story in ecology and behaviour as well as morphology; evolution is holistic and if the package works adequately, though maybe imperfectly, it is good enough for now.

Fossil gannets/boobies

More than 20 fossil species belonging to *Morus*, *Sula* and other, now extinct, genera have been named from the sub-Order Sulae. Fossil sulids are abundant in the Oligocene, Miocene and Pliocene deposits of America and a detailed account is beyond present scope. Specialists should consult Warheit (1990). With the exception of the North Pacific and Romanian fossils all sulids have been recovered from deposits that are within the current geographical range of Recent sulids. However, the absence of present-day sulids from the North Pacific, from which fossils have been recovered, is puzzling.

There used to be many more sulids than there are now. Some, such as *Morus magnus* from the late Miocene of California, were exceptionally large whilst others were as small, or smaller than, the smallest booby of today, which is the male red-footed booby of the Central Pacific region.

The older groups, such as the ancient Plotopterids and Pseudodontornis died out long before man became a threat. More recently, however, vast numbers of seabirds, including sulids, have been wiped out. Steadman (1989) remarks that fossils

from archaeological sites have extended the known ranges of several extant species by thousands of kilometres. Abbott's booby (q.v.) is a good example. Thus some sulids were formerly much more widespread than they are now.

The oldest fossil sulid is *Sula ronsoni* Milne-Edwards from the early Oligocene, more than 30 MYA, followed by *S. arvernensis* Milne-Edwards late Oligocene. It differs from modern sulids in having four notches in the sternum, a primitive condition seen also in the fossil frigatebird *Limnofregata* (q.v.). Harrison (1975) places *S. ronsoni* in the Phalacrocoracidae and proposes *Empherosula* for *S. arvernensis* though Olson (1985a) queries both proposals. Additional fossil species from the Miocene and Pliocene of California and Florida have been put in the modern genus *Sula*. Fossil species of gannets *Morus* occur in the Miocene of California, Pliocene of Florida and of the mid-Atlantic coast of the USA. *Morus reyanus* Howard occurs in the late Pleistocene of California. Most of the many fossil sulids of the mid-Miocene and lower-Pliocene of Maryland, Virginia and North Carolina appear to be *Morus* rather than *Sula*.

The genus *Microsula* comprises two small sulids from the mid-Miocene of France and Maryland. Olson suggests that these two could be conspecific and that *Microsula* may be a small form of *Morus* unworthy of generic status.

Based on proportions of wing bones, three additional genera have been recognized: *Miosula* and *Palaeosula* from the Miocene and Pliocene of California, and *Sarmatosula* from the Miocene of Romania; but Warheit puts all of them in the genus *Morus*.

From Cape Province, South Africa, come fossil sulids of the early Pliocene, including a species of *Sula* about the size of a small red-foot. This is much smaller than the African gannet—the only extant sulid in that region and one for which no ancestor has been found.

Recently a new, extinct, large sulid has been found on Lord Howe and Norfolk Islands and named the Tasman booby *Sula tasmani* n.sp (Van Tets *et al.* 1988). It was found below charcoal of 800 years before present (BP) along with remains of the Polynesian rat, which may have been implicated in

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the booby's demise. The authors speculate that it may have been the species recorded in May 1788, in 'prodigious numbers', nesting on the ground and hitherto assumed to have been the masked booby, but in fact nesting at the wrong time of year for that species. It was described as very large and fat.

In the Society Islands recent fossils include the brown and red-footed boobies, neither of which now breed there. An exciting discovery (Steadman *et al.* 1988) concerns a new sub-species of Abbott's booby (Sp Acc) and a significant extension of this rare booby's previously known range. They describe the now-extinct *Papasula abbotti costelloi* from Tahuata and Hiva Oa (Marquesas), a 4,800-km eastwards extension even from the Solomons, and bones of the extant Abbott's booby *P. a. abbotti* from Tikopia in the Solomon Islands (P O), itself an eastward extension of 6,400 km from its only current breeding place (Christmas Island I O). Formerly, it was distributed across the Indian Ocean and into the S.W. Pacific and has suffered a massive decline at man's hand. Steadman *et al.* (1988) place human settlement of the Marquesas at least 2,000 years ago and *P. a. costelloi* was probably still extant *c.* 1,000 years ago. However, *P. a. abbotti* on Tikopia may not have long survived Polynesian settlement. The age of the layers in which it occurred have been radio-carbon dated to 2,680 years BP. Thus on many oceanic islands throughout a vast stretch of the southern Pacific the most massive extinctions occurred in the Holocene, coincident with the arrival of man, who eventually occupied nearly all of the 266 islands and atolls of Polynesia.

Finally, there is the mysterious 'Slud's booby' of the Pacific Cocos Island (see Nelson 1978b: 760).

Cormorants/shags

Cormorants and shags pose by far the most complicated problems within the Order. They have variously been allocated between one and nine genera and 26–40 species. Species are treated binomially in many works and trinomially in others. The blue-eyed, southern ocean shags, with their several endemic island forms, have caused much disagreement about sub-species and vernacular and scientific names (Sp Acc). Since Murphy's

(1936) pioneering work, Siegel-Causey's (1988) osteological evaluation is accepted by some as the basis for possible revision of the group; it provides new insight into the higher-Order relationships, though some systematists may be unhappy with its large number of species and may query the methodology. Van Tets's (1976) classification based on comparative-behaviour studies provides an interesting parallel.

The most significant issue concerns the number of sub-families and genera. All cormorants and shags, sometimes with the exception of the flightless cormorant, have commonly been placed in the genus *Phalacrocorax*. An alternative view has put the small, long-tailed cormorants in the genus *Microcarbo* (sometimes in *Haliastur*). But more fundamental is Siegel-Causey's proposal² to divide the Phalacrocoracidae into two sub-families, the 'true' cormorants (Phalacrocoracinae) and the shags (Leucocarboninae). Thus he proposes two sub-families, nine genera and at least 35 species, possibly 37. This classification is based on characters such as shape and position of the cavity containing the nasal salt gland, nature of the skull bones (denser or more pneumatic) and degree of preference for a marine habitat (shags) against estuarine or inland waters. A feature of perhaps dubious value is foot colour: Phalacrocoracinae have black legs and feet, *Leucocarbo* and *Nesocarbo* shags pink feet and *Stictocarbo* yellow feet (Kennedy *et al.* 1993).

Siegel-Causey used 137 osteological characters to construct a hypothetical family tree. The problem lies in deciding which similarities reflect relationship rather than convergence. In his analysis the Phalacrocoracidae is a single-rooted (monophyletic) family in which all members possess a terminal hook to the bill. The characters supporting the division into shags and cormorants are plumage, external morphology, osteology and behaviour. The true cormorants (16 species) show 10 definitive osteological characters, six of which are not found in any other taxon and are thus unambiguous. They relate to the muscles of the jaw, the strength and flexibility of the distal part of the wing and to hind-limb action. These characters may be related to a tendency for cormorants to show less-sustained flight and to feed in deeper water. He

divides the cormorants into four genera: *Microcarbo*, *Compsohalieus* (new), *Phalacrocorax* and *Hypoleucos*.

Microcarbo (5 species)—the small cormorants—is the most distinctive genus of the entire family, containing the long-tailed (*M. africanus*), crowned (*M. coronatus*), Javanese (*M. niger*), little pied (*M. melanoleucos*) and pygmy (*M. pygmaeus*). All are distinguished by 16 osteological characters, six unambiguous, relating mainly to feeding adaptations.

The remaining three genera of cormorants are larger birds, sharing similar morphology and behaviour and six osteological characters, one unambiguous (related to wing-action).

Compsohalieus (4 species)—Brandt's (*C. penicillatus*), flightless (*C. harrisi*), bank (*C. neglectus*) and black-faced (*C. fuscescens*)—are marine cormorants previously rarely grouped together. They are heavy-bodied, deep and strong divers with some shaglike characteristics, restricted to islands and coasts near upwellings, where they become locally abundant. Otherwise they have limited distribution and do not disperse far.

Phalacrocorax (large) and *Hypoleucos* (medium or meso-cormorants) form a monophyletic group established by bill shape, the musculature of the distal part of the wing, plumage and behaviour.

Phalacrocorax (2 species), the genus to which even a quite recent classification (Dorst and Mougín 1979) ascribed all extant cormorants and shags, in Siegel-Causey's scheme contains only the great (*P. carbo*) and Japanese cormorants (*P. capillatus*). It is distinguished by nine characters, five of them unambiguous, relating to muscles of the palate, nasal gland and flight. Most characters are related to feeding in shallow water or the upper layers of deeper water. The great cormorant has such a vast distribution that it is likely to be a superspecies or, alternatively, currently recognized sub-species may be species.

Hypoleucos (5 species) is a varied genus of entirely dark, middle-sized cormorants with some members forming dense, often huge colonies. It consists of the pied (*H. varius*), Indian (*H. fuscicollis*), little black (*H. sulcirostris*) and, in the neotropic (*H. olivaceus* = *brasiliensis*) and double-crested (*H. auritus*), the only New-World meso-cormorants, whose geographical sub-divisions are apparently much greater than currently recognized.

The sub-family Leucocarboninae, accommodating the remaining five genera containing 20 species, are all shags united by seven characters, four unambiguous and related to jaw movement and wing action.

Leucocarbo (3 species)—guano shags. The Socotra cormorant/shag (*L. nigrogularis*) (most primitive) most resembles the Cape shag (*L. capensis*) and both are more like cormorants in outward appearance compared with other Leucocarboninae. The guanay (*L. bougainvillii*) is the most derived member.

Notocarbo (4 species)—from 'southern' (*Noto*) and 'black' (*carbo*), is a new genus for which Siegel-Causey designates *N. atriceps atriceps* the type. It is identified by a particular configuration of a bone of the skull (the mesethmoid) and contains some of the blue-eyed shags, a particularly pelagic group for which no pre-existing genus was available. Much vexation has previously centred around the specific names *atriceps* and *albiventer* variously referred to as king, imperial or blue-eyed shags but Siegel-Causey could not distinguish between them either by osteology or behaviour and he refers them to *atriceps*. *Notocarbo* includes, as full species, the imperial, South Georgian (*N. georgianus*), Antarctic (*N. bransfieldensis*), and Kerguelen (*N. verrucosus*) shags. The rank and relationships of forms currently regarded as sub-species (*N. atriceps nivalis*; *N. a. melanogenis* and *N. a. purpurascens*) have not yet been determined in this new classification.

Eulocarbo and *Nesocarbo* are externally similar to the *Notocarbo* shags, but osteologically distinct.

Eulocarbo (5 species)—within which relationships are at present tentative—contains the New Zealand blue-eyed shags—king, bronze or rough-faced (*E. carunculatus*), Stewart (*E. chalconatus*), Chatham (*E. onslowi*), Auckland (*E. colonsoi*) and Bounty (*E. ranfurlyi*).

Nesocarbo (1 species) the Campbell shag (*N. campbelli*). Traditionally this has been closely linked to the other New Zealand blue-eyed shags, particularly Auckland and Bounty, but Siegel-Causey shows it to be distinctive.

Stictocarbo (7 species)—a monophyletic group with four unambiguous characters—comprises the 'cliff' shags. They are greyer and more upright with a distinctively flattened head and share several

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convergent features with the more massive cormorants. The core group contains the rock shag or Magellanic cormorant (*S. magellanicus*), pelagic shag/cormorant (*S. pelagicus*), red-faced shag/cormorant (*S. urile*) and European shag (*S. aristotelis*). These species are dark and tend to feed in upper-layer coastal waters. The most derived species are the red-legged shag/cormorant (red-footed cormorant) (*S. gaimardi*), spotted (*S. punctatus*) and Pitt (*S. featherstoni*) shags.

Some of the above relationships have been borne out by DNA hybridization work (Sibley and Ahlquist 1972). As Siegel-Causey points out, however, the weight that can be placed on osteological evidence depends on how far these features are mere functional adaptations rather than indices of relationship. When all characters except cranial ones were analysed the resultant relationships within genera were identical to those obtained by including cranial characteristics. However, analysis of cranial characters alone gave a very different picture, showing the *Leucocarbo* shags to be polyphyletic and indicating that head characters are indeed particularly prone to convergence.

On the basis of behaviour, Van Tets (1963) divided the cormorants into macro-, meso- and micro-, and the shags into king and cliff. In the king shags, male advertising (a sexual display) consists of a single 'throwback' (a head movement) with 'gargling' in five species, plus rhythmic wing-flicking in one, and a single throwback without gargling in another. In the remaining species, males wing-flick but with no throwback or gargling. In the cliff-shags, male advertising consists of non-vocal, rhythmic wing-flicking with no throwback in four species and non-vocal, rhythmic, upwardly directed head movements (darting), with throwback, in one.

In the macro-cormorants, which in this classification embraces only the great and Japanese cormorants, male advertising consists of wing-flicking and throwback-with-gargling. In four of the meso-cormorants, males advertise by means of wing-flicking with vocalization. The behaviour of the micro-cormorants is little known.

Fossil cormorants/shags

An exciting fossil find was several pelecaniforms, related to cormorants, of the now-extinct flightless

family Plotopteridae (Olson 1980). More recent fossil cormorants have been discovered, for example, in South African Pliocene deposits, and in Florida late Pliocene deposits held 137 skeletons of a fossil cormorant closely related to the extant Brandt's (Emslie and Morgan 1994). Emslie (1995a) named it *Phalacrocorax filyawi*, and suggested that the cormorants died in a single catastrophe, such as a 'red tide', and that these and other seabirds from the Pliocene support evidence that at that time the Florida Gulf was highly productive (cold water upwelling).

Warheit (1992) demonstrates, for the North Pacific, that not until 18–12 MYA did fossils contain any seabird taxon with present-day representatives. Cormorants do not appear until 13–8 MYA by which time conditions in the eastern North Pacific were probably similar to today's and it was during this period that the cormorants showed their initial radiation. This was not sustained and cormorants are missing from the fossil record of 7–4 MYA.

Anhinga/darter

The darters–anhingas form a small, closely related group to which different authorities have assigned either family or sub-family rank, usually placed close to or within the cormorants. But despite their strong resemblance they differ in structure and behaviour (Sp Acc). Sibley and Ahlquist (1990), on the basis of DNA–DNA hybridization, greatly altered existing avian classification and in their scheme anhingids come nearer to sulids than cormorants.

Anhinga (one species) are the American form and darters represent the Old-World form. Darters are sometimes regarded as three species (African, Oriental and Australian) or as one superspecies.

Fossil anhinga/darter

These have been discovered from the late Miocene, early Pliocene and late Pleistocene. Becker (1986) reassigned what was formerly considered a fossil cormorant to conclude that anhingids have been separate from cormorants for 30m years or more. Emslie and Morgan (1994) suggest there were two lineages of anhinga in the fossil record of Florida: 'one line of

large anhingas, beginning with *A. grandis* in the late Miocene, existed until the end of the Pleistocene. A second line of small anhingas is represented by the living species'. Recently Mackness (1995) described an early Pliocene anhingid (*Anhinga malagurala*); the smallest yet described and the oldest fossil darter from Australia. Campbell (1996) describes a new species of giant anhinga from the late Miocene of lowland Amazonia.

Frigatebirds

These may be considered distinct enough to merit sub-Ordinal status. They are characterized by extreme aerialness (prolonged soaring) with associated skeletal specializations (distinctive wing proportions, modified pectoral girdle, light bones, greatly reduced legs and feet, with vestigial webs). They are almost unable to walk and are behaviourally highly distinctive. Olson's (1977) discovery of the Eocene *Limnofregata* (see below), by erecting a new genus, requires a new definition of the family and he proposed the following: Order *Pelecaniformes*; Sub-Order *Fregata*, Family *Fregatidae*; Sub-families *Fregatinae* (new rank) and *Limnofregatinae* (new sub-family); *Limnofregata* (new genus) *Limnofregata azygosternon* (new species).

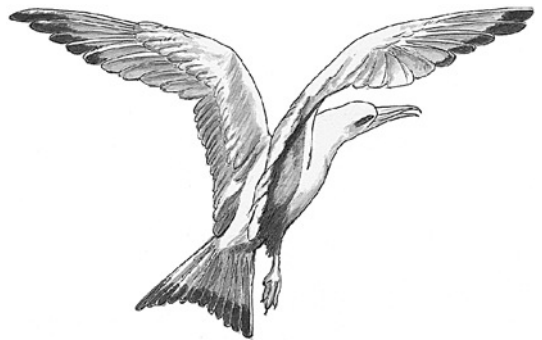
The extant frigatebirds form a single tightly knit genus *Fregata* containing five clearly separate species, namely *F. minor* (great frigatebird), *F. ariel* (lesser or least), *F. aquila* (Ascension), *F. magnificens* (magnificent) and *F. andrewsi* (Christmas). At one time only two species were recognized; the four larger lumped under *F. aquila* and the lesser, once even placed in a separate genus *Atagen*. Now there is a suggestion that the lesser may be divisible into two species. The great and magnificent frigatebirds have not been immune from the splitters (Sp Acc). Mathews (1914) named most of the species and races yet lumped the great and magnificent frigatebirds under Gmelin's name *Pelecanus minor*, who in turn presumably followed Linnaeus (1758) in placing frigatebirds in the same genus as pelicans. This gave rise to the contradiction between the scientific name *F. minor* (because it was smaller than a pelican) and the vernacular name, great frigatebird (del Hoyo *et al.* 1992). The confusion is compounded because there *is* a smaller frigatebird,

the lesser, which often nests on the same island as *F. minor*. Later, the Caribbean population of Mathews's 'species' (above) became *F. magnificens*, the specific name *minor* being then transferred to (great) frigatebirds from the eastern Indian Ocean.

Frigatebirds are still closely enough related to show marked similarities in plumage. The Ascension frigatebird has presumably been isolated for some considerable time but the male is not readily distinguishable from the magnificent. Some individuals show areas of white which, particularly in the female, clearly relate to patterns typically found in other frigate species. Similarly, the colour of the orbital ring in the female Ascension resembles that of the magnificent and of some populations of the great frigatebird. Again, female magnificents quite closely resemble female Christmas frigatebirds. However, in the two species which most often breed in close proximity (great and lesser frigatebirds) there are considerable differences in size, plumage and behaviour.

Fossil frigatebirds

Until recently the only known fossils were from the Pleistocene, and were of extant species. Then Olson (1977) identified a fossil from the Eocene (Wyoming) and proposed the name *Limnofregata azygosternum* (see above). This frigatebird was already sufficiently specialized to be recognizably akin to modern forms (Figure 1.3) but its bones were heavier. Olson suggests it was better suited for flapping flight and better able to alight and take-off from land and water.



1.3 *Limnofregata*; a reconstruction of a fossil (Eocene) frigatebird. (Re-drawn from Olson 1977.)

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Even more recent fossils from the Society Islands (Steadman 1989) include great and lesser frigatebirds, which no longer breed there.

Tropicbirds

As with frigatebirds, these may be considered distinct enough to merit sub-Ordinal status *Phaethontes*. They differ from other pelecaniforms in their massive pectoral development, atrophied pelvic region, lack of bare gular skin, slitlike nostrils, greatly reduced legs, and downy hatchlings; but, like them, have totipalmate feet, salt glands within the orbits and no incubation patch.

Tropicbirds may constitute a single superspecies, though usually, as here, they are treated as three species within a single genus. These species have often been divided (probably mistakenly) into 12 taxa. The most visually distinctive race is the striking golden bosunbird of (mainly) Christmas Island (I O) but even this may be a colour morph. Tarburton (1989) found that the red-tailed tropicbird grades in size, intensity of pink suffusion, and measurements between north and south in the Pacific but in neither regions is it clearly separable from those in the centre or elsewhere and he rejects sub-specific status. Similar considerations may well apply to the three races assigned to the red-billed.

Fossil tropicbirds

Although tropicbirds may be at least as old as other pelecaniforms, there was no Tertiary fossil until

the discovery of *Heliadornis ashbyi* from the mid-Miocene, Calvert Formation, Maryland (Olson 1985b). This fossil species has been discovered, also, from a contemporaneous site in Belgium (Olson and Walker 1997). Olson believes it represents a distinct line not ancestral to present-day forms. It has a well-developed pectoral crest and poorly developed acromion process (part of the scapula); both features occur in frigatebirds but not pelicans or sulids. A new species *Heliadornis panethydicus* has been described from Australia, late Miocene (Mlikovsky 1997).

A fossil *Prophaethon shrubsolei* Andrews 1899, from the Lower Eocene London clay, was originally allocated, by Andrews, to the Phaethontidae. Harrison and Walker (1976) then elevated it to a new family Prophaethontidae within a new Order, *Prophaethontiformes*, on the grounds of its links with the procellariiforms and charadriiforms. Olson disagreed but affirms its considerable differences from *Phaethon* and suggests it should be placed in the Sub-Order *Phaethontes*. It has a long, open nostril similar to that of embryos and juveniles of modern pelecaniforms, whereas most adults have partly or completely ossified nostrils. The primitive open condition is found, also, in the Eocene frigatebird *Limnofregata* (q.v.)

1. This number is controversial since it depends on how the blue-eyed shag group is classified.
2. Although the more conventional classification of cormorants/shags is used in this volume, revision along Siegel-Causey's lines may eventually take place.

Introduction

These introductory remarks apply also to the behaviour sections of the General Family Accounts.

Many ethologists see little point in further descriptive comparative studies of bird behaviour. Lorenz and Tinbergen long ago established major principles. For example, ritualized behaviour, so evident in pelecaniform display, evolves from simple precursors or 'building blocks'; it is remarkably stereotyped and species-specific; communicative in function; in large part genetically programmed; its form often reflects a balance between conflicting motivations, principally aggression and fear; 'displacement activities' often arise and may themselves become ritualized; ritualized behaviour is often a reliable indicator of taxonomic affinity. Would these principles be any better understood with more examples? Tinbergen argued for more such work but that was long ago and current interest centres on behavioural ecology, on the ways in which behaviour influences breeding success via 'strategies', 'deception' in communication, 'trade-offs', as in parent-offspring conflict and other ecologically related phenomena. Coarse-grained field-behaviour studies with their frustrating inconveniences and variables have yielded to experimental and manipulative work and to computer simulations. In the journal 'Animal Behaviour' actual behaviour patterns are almost never illustrated or even described. The behaviour is merely a cipher to be subjected to ever more sophisticated statistics and most readers may have no idea what it looks like.

Behaviour underpins comparative work; may be useful in wider syntheses; illuminates evolutionary

processes; can aid conservation (Sutherland 1998); aids taxonomy (see, for example, Kennedy *et al.* (1996) who show that pelecaniform displays are as useful as morphology and genetics in establishing homologous relationships); helps in interpreting ecology and aids our understanding of how seabirds, basically unintelligent, nevertheless conduct highly complex social lives. These comments apply mainly to ritualized, communicative behaviour involved in breeding, and to feeding and foraging. The minutiae of preening, scratching, stretching, defaecating, drinking, yawning, ordinary walking, swimming, shaking, panting, etc. can become tedious and space-consuming. They receive little attention here.

The term 'behaviour' is often loosely used. Many important aspects of a bird's life, such as natal philopatry, site and mate-fidelity, sociality, the frequency with which the young are fed and much else, are strictly not behaviour if this is defined as voluntary motor movement, thus excluding autonomic activities. Rather, they are aspects of ecology. The *actual* behaviour is walking, standing, flying, displaying or whatever (there is a grey area here but the main point stands). Regurgitation is behaviour but the frequency of feeding young is an ecological parameter.

Behaviour is underpinned by physical features and physiology. The former differentially facilitates various types of movement such as walking, swimming, and flying which accordingly play a greater or lesser role in rituals, whilst the latter, via the effects of hormones, relates to sexual and aggressive display (Lormee *et al.* 2000). Balthazart (1983)

provides an exhaustive review of the hormonal correlates of behaviour.

The more closely species are related the greater the similarity in their behaviour, as for example in the blue-footed and Peruvian boobies. But adaptive radiation into different environments with different selection pressures has engendered marked behavioural divergences, more in some families than in others. Frigatebirds and tropicbirds are small, homogeneous families in which their respective species have similar lifestyles in similar environments and their overt behaviour varies little. But cormorants and shags form a large family with a wide range in distribution and ecology. Their overt behaviour is more varied, although aspects largely independent of lifestyle, such as courtship, retain clearly homologous components. Homology is an essential concept in comparative studies and behaviour is a vital tool in such investigation.

The main pelecaniform families contain 'core' species, similar in ecology and behaviour, and divergent species. For example, masked, blue-footed and Peruvian boobies are behaviourally similar whereas neither the gannets nor Abbott's booby much resemble them. Great white, Dalmatian, American white and Australian pelicans are in many respects similar; the brown differs. In the cormorants, groups such as the blue-eyed shags have exceptionally similar behaviour.

Commonly, several members of the same family and two or more families coexist on the same island or group. Before the advent of man there would have been many more species and immensely greater numbers (see Steadman 1989). Under these circumstances differences in flying, walking, swimming, etc. effectively partition feeding and nesting resources; the pelecaniforms exhibit an exceptionally wide spectrum of foraging, feeding and breeding behaviour.

This chapter summarizes and compares the behaviour of the six pelecaniform families and discusses some general behavioural topics. Within-family comparisons are dealt with in the General Family Accounts and species-specific behaviour in the Species Accounts. Most specific references applicable to the present chapter are to be found there.

General behaviour/ecology

Comparative display

Detailed comparative studies of display involving large seabird taxa are relatively few. For the pelecaniforms they include van Tets (1965) on the origin of some displays in pelicans, cormorants and sulids; Nelson (1970, 1978b) on territorial and courtship display in sulids; Warheit (1990), a particularly rare contribution in its sophisticated analysis of behaviour in relation to sulid morphology; and the complex analysis by Kennedy *et al.* (1996) of a particular stereotyped sequence of movements found in pelecaniform display. Outwith the pelecaniforms, Tinbergen's (1959) comparative study of gull behaviour provided an early stimulus.

Sexual dimorphism

In birds, size differences between the sexes have been attributed to intraspecific competition for mates, female selection or as an adaptation to different feeding niches (e.g. Zahavi 1975; Nelson 1978b; Mueller 1990; Guerra and Drummond 1995). In albatrosses, penguins and gulls, males are larger than females and similarly in pelicans, cormorants and anhingids, but in frigatebirds and most boobies females are larger than males. Whilst in seabirds, isomorphism (sexes looking alike) may be an advantage in equally shared breeding duties such as site-defence, there is dispute about the evolution and functions of dimorphism in size and especially of reversed sexual dimorphism (RSD). RSD has evolved several times; four times among aerial pursuit predators (the diurnal raptors, skuas, some boobies and frigatebirds). This does not explain why it is males that are the smaller sex.

Building on Darwin's theory of sexual selection (males competing for females and females choosing between males) some studies have shown that females may prefer males with especially well-developed secondary sexual characters (see Majerus 1986 and references) but nobody has studied this in pelecaniforms.

Jehl and Murray (1986), drawing particularly from shorebirds, proposed that where males have to compete for females and use aerial display in

territorial advertising and courtship display, smaller and therefore more agile males should be at an advantage. Via sexual selection, this should lead to RSD. Indeed, one of their main points, following Power (1980) is that 'the initial morphological divergence between the sexes cannot arise from ecological selection but must be the result of sexual selection'. Once initiated, ecological factors come into play and partitioning of resources may then result. I suggested (Nelson 1978b) that in sulids, the pelecaniform family in which RSD is most marked, a major advantage lies in opening up different feeding niches for the sexes but its function may be composite. Indeed, in the blue-foot but in a different location, Guerra and Drummond (1995) provide evidence against the proposition that, in feeding the young, there is division of labour based on sex-dimorphism with the large female feeding further offshore and bringing larger payloads for the middle and later stages of chick growth. Gilardi (1992), however, reached somewhat similar conclusions to mine about the markedly sexually dimorphic brown booby. He found that (as in the blue-foot) females foraged further from shore than males; the sex ratio was strongly male biased within $c. 20$ km of the colony but female biased beyond $c. 90$ km. He linked these differences to sex-role partitioning, suggesting that selection on females for increased chick provisioning may have led to greater size and foraging range.

RSD could serve also in pair formation via aerial display. The blue-foot, in which RSD is most marked, displays in flight and the brown booby, also, is notably aerial in display whilst the often-sympatric masked, in which the sexes differ less, is not. The gannets, in which the sexes are much alike, show nothing comparable to the aerial courtship of the blue-footed booby. However, the red-footed booby, in which RSD is quite marked, is not notably aerial in courtship (although it is particularly prone to catch flying fish whilst in the air). In cormorants RSD is comparatively slight and even in species such as the red-legged cormorant, which has aerial display, there is little male-female disparity in size.

However sexual dimorphism arose, it must have ecological consequences. The spectrum and size

of prey in the male blue-footed booby cannot be the same as in the female. Raptors and RSD have received special attention but are unlikely to provide a unifying hypothesis. Nevertheless, Newton's (1979) demonstration that sexual dimorphism is most marked in those groups, such as some falcons, whose prey is agile and fast, and least marked if at all in carrion-eaters and scavengers, indicates the nature of some of the factors involved (see also Paton *et al.* 1994). Could a modified version apply to pelecaniforms?

Mueller (1990) opposes the idea that RSD is explicable in terms of differences in foraging/feeding abilities. He proposes that large and dominant females are selected where aggressive males could damage them. Regardless of its merit where raptors are concerned, it is inappropriate for pelecaniforms. He suggests that 'where males compete vigorously for access to females, sexual selection favours large size in males and small size and perhaps subordination in females...'. Precisely the opposite is true, for example, in frigatebirds, in which males do compete vigorously (by display) for females but are smaller than them. The fact is that in pelecaniforms the families show all possible states: males bigger than females, females bigger than males and sexes equal. The utilization of different feeding niches remains, in my view, of major importance. As Jehl and Murray (1986) imply, the combination of factors directing sexual dimorphism in birds may be expected to differ from group to group.

Locomotion

The ability to walk easily has facilitated ritualized, locomotion-based displays and these are particularly important in pelicans and sulids. Tropicbirds and frigatebirds are almost helpless on the ground; the former display in the air and the latter in trees or bushes. Walking and perching ability has a marked effect in determining nesting habitat: cormorants, anhingids, pelicans and boobies can perch, jump, hop, walk, and flap-climb, and can use a wide range of nesting habitats which are barred to the other two families. Whilst the bill is used as a climbing aid by cormorants, anhingids, sulids, pelicans, and frigatebirds, it is always as a hook or lever and never, even

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in a crisis, for grasping. Cormorants, anhingids, and sulids especially but also pelicans use ritualized postures to precede, accompany or follow hops or walking during territorial behaviour or pair interactions. When swimming on or below the surface all peleceniforms use alternate and simultaneous foot-propulsion whilst, in addition, sulids and tropicbirds use their partly opened wings underwater—which probably influences wing morphology (see Chapter 1). Synchronous thrusting with the feet with wing-beating is usual when taking off from land or water.

All peleceniforms are excellent fliers, between them employing sustained flapping, flap-gliding and soaring, and lacking only the true dynamic soaring of albatrosses. Primarily they fly into or across head winds (see Spear and Ainley 1997a, 1997b for seabird flight in relation to wind direction and wing morphology). Wing-form and body-mass strongly affect foraging/feeding methods with important effects on breeding biology.

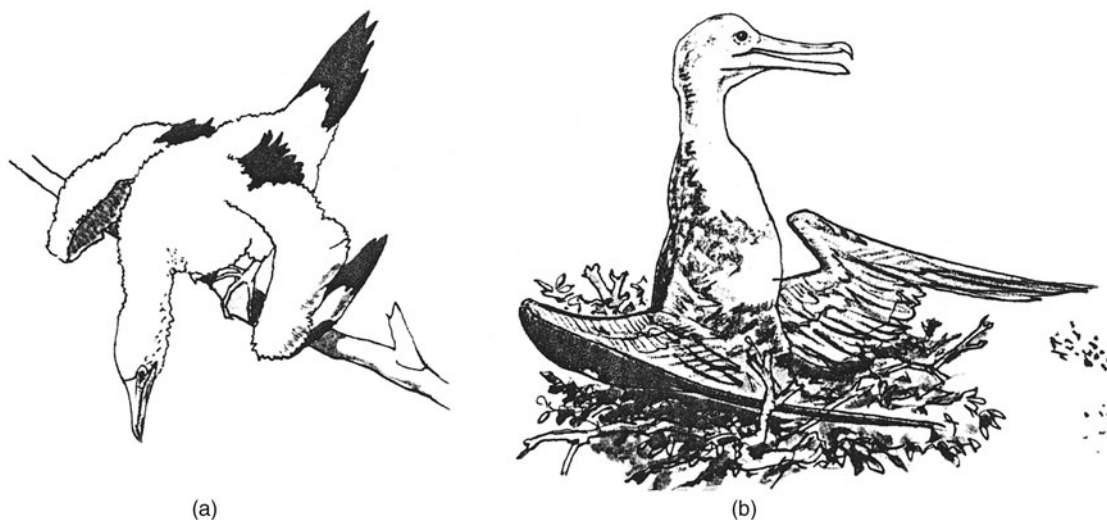
Body care

All peleceniforms preen and oil; all scratch directly (leg under wing) though frigatebirds scratch indirectly too. All wing-stretch but none, except as

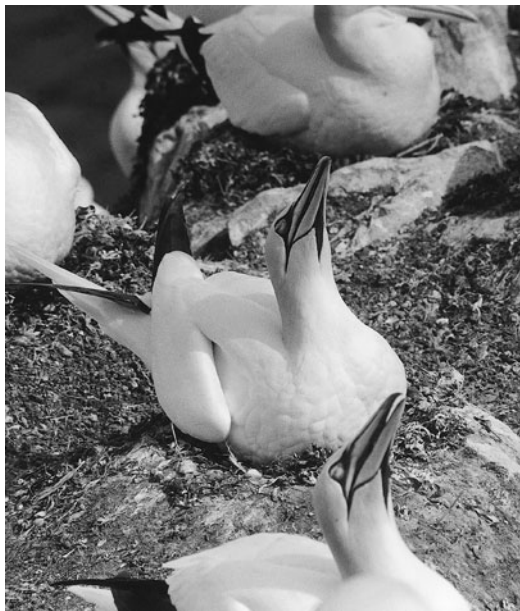
chicks, uses the 'both wings arched' of gulls and terns. The behaviour used to regulate body temperature varies with family. All employ energy-saving postures (head hanging (Figure 2.1(a)) or propped on substrate, wing-drooping) and raise dorsal feathers to allow heat to radiate out. All except tropicbirds use gular fluttering and pant and gape (Figure 2.2.) Sulids (and possibly pelicans, cormorants and anhingids though not specifically recorded) excrete onto their webs for evaporative cooling. Adult peleceniforms usually sleep with head in scapulars but frigatebirds often eschew this.

Only cormorants and anhingids use the spread-winged posture to dry their wing feathers after repeated submergences and only frigatebirds 'sun-soak' in searing heat, (Figures 2.1(b) and 2.3) wings upturned, to redress the deformity of flight feathers whose keratin has been altered in its molecular structure by the stresses of continuous soaring flight (Houston 1980). Sulids and tropicbirds sit with loose, tips-crossed wings to the sun, possibly to aid heat-loss.

Bathing differs but rhythmic beating of the water with the wings, head-ducking, and rolling onto one side occur in all except frigatebirds which rarely settle on water.



2.1 Body-maintenance: (a) energy-conserving resting posture, red-footed booby chick. (b) 'sunning' posture in juvenile great frigatebird (the heat re-shapes feathers deformed by prolonged soaring). (From Nelson 1980, drawings: J.P. Busby.)



2.2 Atlantic gannets controlling body temperature by radiating heat from facial and gular skin.

All peleceniforms drink but only frigatebirds do so by dipping to the surface in full flight and only pelicans pouch water in quantity. Frigatebirds sometimes drink communally at freshwater pools but like the rest of the Order can drink seawater and excrete salt from the nasal gland.

Loafing, roosting and 'clubs'

Gregarious loafing and roosting is characteristic of peleceniforms. In all except tropicbirds, resting and roosting, often with other species, occurs at traditional sites and in various habitats (GFA; Sp Acc). Pelicans and cormorants especially, may fly considerable distances to particular nocturnal roosts. Outside the breeding season roosting at or near breeding colonies is common in some cormorants, boobies and frigatebirds, in which case a colony may always be 'occupied' though not necessarily by its own breeders. Equally, colonies may be entirely deserted outside the breeding season, as in Atlantic and Australasian gannets, some seasonally breeding booby, cormorant and anHINGID populations, some pelicans and some tropicbirds. But the nearly continuous breeding (successive groups) of some pop-

ulations of boobies, pelicans and tropicbirds means that even though failed or successful breeders may disperse, some individuals are always present.

The tendency of off-duty breeders with eggs or young to loaf, preen and roost in gatherings near to or within a breeding colony is little documented though important in interpreting the functions of individual absences, for it is often assumed that these represent foraging time. Non-breeders, too, may loaf and roost in or near to breeding groups.

There is no firm evidence that roosts act as communication-centres for transmitting foraging information.

Clubs, *sensu* social gatherings where incipient courtship and territorial activity occurs, appear to be well developed only in some sulids, especially gannets. This may relate to the adaptive value of practice in site-establishment and pair-formation. There is a marked difference between a roost or even a loafing aggregation, where birds merely rest or preen, and a gannet club, which can be extremely active and, in the range of its ritualized activities, more resembles a breeding colony.

Foraging and feeding

Distances

Whilst all peleceniform families contain species which forage at some distance from the breeding colony and others which, at least occasionally, forage nearby, there are clear differences in typical foraging distance. Tropicbirds and some sulids have the greatest range (several hundred kilometres) followed by frigatebirds, pelicans, and cormorant/anHINGIDS. Even excluding the flightless cormorant, the latter contain species which typically forage within less than 10 kilometres. Whilst marine species forage further afield than freshwater, even the latter may travel more than a 100 kilometres. Foraging distance determines the frequency with which young can be fed and is therefore related to brood size and the rate at which chicks grow, so that cormorants, anHINGIDS, and pelicans have bigger broods of faster growing chicks whilst frigates and tropicbirds have only one chick and seven of the nine sulids rear only one. The two exceptions feed inshore.



2.3 Juvenile great frigatebird 'sunning' to restore shape of deformed flight feathers.

























As well as avoiding long flights, cormorants and anhingids, by diving from the surface rather than from the air, and catching several fish per dive, may spend less energy when feeding. Their strategem depends on comparatively rich local food sources and they are debarred from exploiting areas with poor, patchy and widely dispersed food (GFAs).

Feeding methods

The energetics of feeding are complex (Figure 2.4.) Only cormorants and anhingids have evolved prolonged underwater pursuit (foot propulsion) and only sulids and to some extent tropicbirds plunge deeply from the air, which is perhaps the most evolutionarily advanced feeding method. Wilson *et al.* (1992) interpret the differences in diving behaviour in several taxonomic groups, in terms of physical and physiological characteristics. They note that diving birds differ in the amount of air trapped in plumage and in the amount of body fat. Air makes birds work harder to remain beneath the surface, especially if only slightly under, whilst fat, though

valuable insulation, also increases buoyancy (though not markedly) and adds to the cost of flight. Cormorants expel air from the plumage and do not lay down fat, thus militating against far-foraging flight but facilitating diving. Lack of fat greatly reduces their ability to withstand starvation and gives further advantages to inshore feeding in food-reliable habitats. Sulids and cormorants provide case-studies for assessing the idea that birds which fly far to find food do not then expend much energy in their pursuit diving and vice versa. Most cormorants do not fly far and they do dive deeply and pursue extensively, and the deeper they dive the faster they then swim, thus maximizing the area searched. Sulids fly far and though they may dive deeply this is achieved cheaply, by plunging. Theoretically they should not then use their wings (which are long) to swim underwater, but in fact they do so to a limited extent. Moreover, although they have less air in their plumage than, say, gulls or albatrosses, they do possess extensive air sacs which greatly increase buoyancy, though this is partly nullified by power-diving for which, indeed, the sacs

2.4 Pelecaniform feeding methods.

<i>Family</i>	<i>Deep plunge- diving</i>	<i>Surface plunge- diving</i>	<i>Surface diving, underwater pursuit</i>	<i>Piracy</i>	<i>Communal diving from air</i>	<i>Communal diving from surface</i>	<i>Communal fishing, surface or sub-surface</i>	<i>Scavenging behind fish- ing boats</i>	<i>Scavenging on land</i>	<i>Catching prey in air, (flying fish)</i>
Pelicans		 A		 A			 M	 A	 A	
Gannets/ boobies	 M	 A	 A	 A	 MA			 A		 A
Cormorants/ shags			 M			 A	 A	 A	 A	
Anhingas/ darter			 M							
Frigatebirds				 MA				 A		 M
Tropicbirds	 M	 A								

M=Main
A=Ancillary

are necessary protection. Sulids, therefore, are both far-foragers and deep divers, a dual capacity which removes them from competition with cormorants.

Pelicans especially but also some boobies and cormorants have evolved truly cooperative (as against merely communal) fishing. Only tropicbirds and possibly Abbott's booby are almost always solitary feeders, rarely participating in the mixed-species flocks so characteristic of boobies and frigatebirds and, under special circumstances (as in the Humboldt current) of brown pelicans and guanay cormorants too.

Only frigatebirds specialize in piracy, although some sulids and pelicans steal food opportunistically. Only frigatebirds are immune from food-stealing attacks by other species.

Some cormorants, pelicans and at least one sulid (Atlantic gannet) occasionally forage on foot in mud or shallow water. Only pelicans sometimes scavenge on land, feeding on dead or occasionally live young of their own and other species and on mammals and invertebrates. Although the Order is predominantly marine, all pelicans (except the brown),

many cormorants and the anhingids are wholly or partly freshwater feeders. Sulids, pelicans, frigatebirds and, at least, European shags sometimes scavenge after fishing boats.

Cormorants, gannets, boobies and pelicans, but not frigatebirds or tropicbirds, return from foraging in goose-like skeins, presumably for aerodynamic efficiency. However, only in some pelicans are outward bound flights distinctly organized (see especially American white pelican) though gannets, boobies and cormorants often depart in groups.

Some pelicans and boobies, and perhaps frigatebirds, forage at night. Possibly frigatebirds and red-footed boobies benefit from bio-luminescence of marine prey.

Colonies

With one or two partial exceptions, all pelecaniforms are colonial (see Chapter 3). In all families except the tropicbirds, for which there are sometimes insufficient suitable nest sites, colonies may be

26 Pelicans, Cormorants and their relatives

small or huge. The biggest colonies occur in pelagic feeders with extensive foraging areas and few suitable breeding localities, or in areas adjacent to superabundant food. The colonies of the guanay cormorant (Peru), once reputedly millions on one island, were the biggest and densest within the Order. During their breeding life, individuals of almost all pelecaniforms either move their nest site within the colony, move between different colonies, or the entire colony moves (see Chapter 3). All pelecaniform recruits, with the sole exception of island endemics, may move to a colony other than the one of their birth, to breed for the first time, though natal philopatry is the general rule.

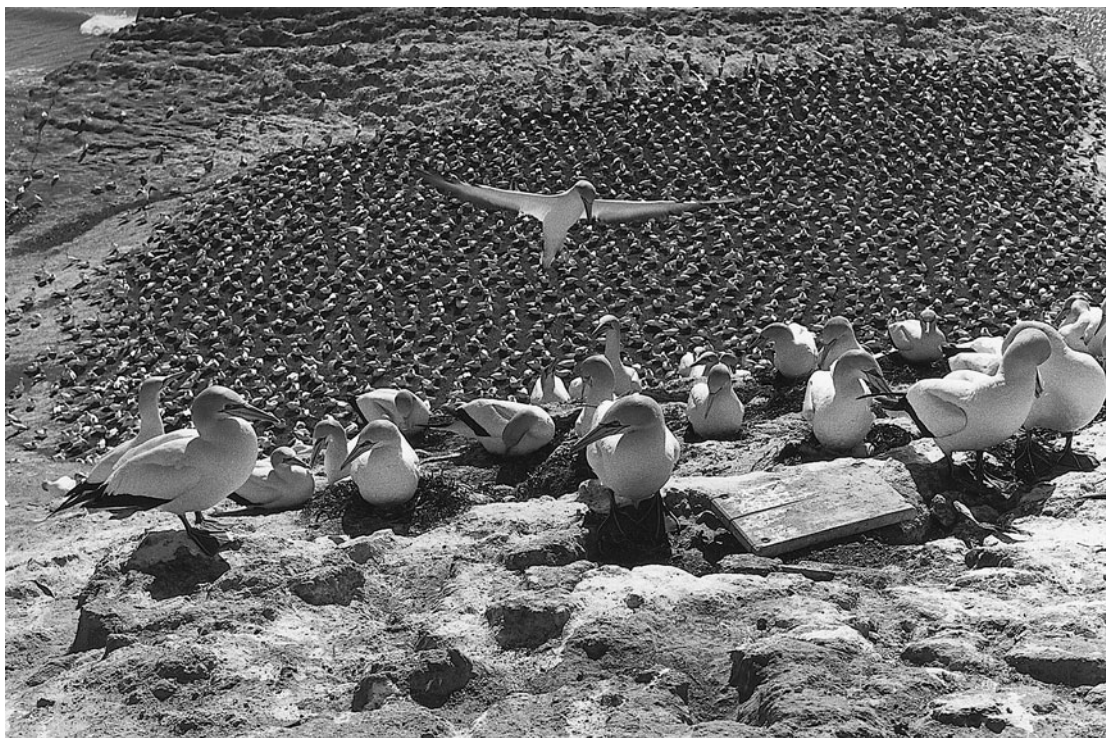
Spacing

Spacing within colonies eg. Figure 2.5 is consistently more species-typical than is absolute colony

size, because, unlike the latter, it is mediated by innate behavioural responses to conspecifics and is highly adaptive. Colony size, by contrast, can vary without penalty provided minimal social requirements are met. Spacing varies with family, species and even locality and is better discussed in the General Family and Species Accounts. The combination of coloniality and territoriality favours highly developed communication behaviour and this is a notable feature of pelecaniform colonies.

Attendance

(See Chapter 3.) Time and energy spent occupying the breeding site is costly. Pre-breeding attendance in pelecaniform colonies relates to: degree of nomadism; climate at the breeding location which may severely restrict the breeding period; capacity to exploit food flushes by opportunistic breeding;



2.5 The Australasian gannet as an example of colonial breeding. Note the high density but regular spacing and the clear edge to the colony with a few non-breeders beyond the fringe.

value of the previously owned site which may be usurped if a bird returns late; ease with which energy costs associated with lengthy pre-breeding attendance can be met and the importance of fidelity to the previous partner. Species such as Abbott's booby and the gannets, with strong site/mate fidelity, tend to show longer pre-breeding attendance.

Pelicans, frigatebirds and sometimes tropicbirds occupy their actual breeding sites only shortly before egg-laying. In fact in some pelicans and all frigatebirds, attachment to a precise site hardens only after initial pair-formation, and the pre-laying period is merely to form and consolidate the pair-bond, build the nest and manufacture the eggs. This may require less than two weeks; some pelicans lay a few days after return to the colony (e.g. Knopf 1979; Evans and Knopf 1993). By contrast, the Atlantic gannet spends months displaying on the breeding site both before egg-laying and after the juvenile has flown, and some cormorants attend, albeit sporadically, for months before laying (Ainley and Boekelheide 1990). These are the extremes and most sulids and cormorants attend only two to four weeks before laying. Cormorants do not usually retain the same site and mate, nor are sites usually limited (though optimal ones may be). Their inshore foraging facilitates frequent visits to the breeding area, especially in resident species. But no peleciform except sulids spends much time in concentrated pre-breeding territorial display.

Tropicbirds often breed a-seasonally and competition for holes is exacerbated by low breeding success which returns failed breeders to the site-seeking pool. And their pelagic foraging makes semi-continuous hole-guarding difficult. Often, it is a matter of returning to the colony when ready to breed and quickly acquiring site and mate. Late return minimizes danger associated with land but, more importantly, optimizes foraging efficiency by reducing the period over which a bird must travel between nest-site and food source.

In sum, unless there are marked benefits, peleciforms spend little time attending and defending a breeding site except immediately before a new breeding attempt. However, many sulids,

cormorants, anhingids and perhaps frigatebirds attend the colony, more or less desultorily, to loaf and roost. Post-breeding pelicans, Atlantic and Australasian gannets, and tropicbirds largely or entirely desert it.

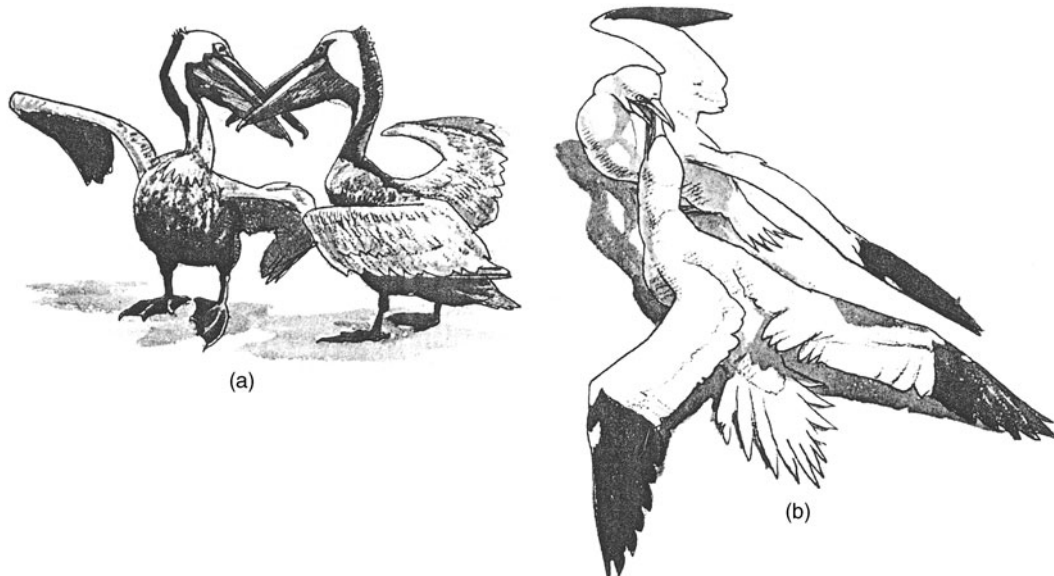
Territorial and sexual behaviour

In a simple case, such as the Atlantic gannet, the male prospects for a site, claims it, hardens his attachment and then defends it by fighting, threat and ritualized site-ownership display. From it he displays to attract a female from the pool of prospectors. Male and female interact ritually (with clearly aggressive elements involved), form and cement a pair-bond and breed. Once bonded, the female shares defence of the site which is retained for successive breeding attempts. In other peleciforms this sequence is not so clear-cut.

There are three general procedures. First, males select and then display singly on a site on which they eventually breed. Most sulids, a few cormorants, and anhingids may retain this in one or more subsequent years but most peleciforms do not (gannets and Abbott's booby are exceptional in retaining a precise site throughout their breeding life). Second and uniquely, male frigatebirds settle in clusters on sexual display sites but if they fail to attract a female move to another display group. They establish a breeding site (used for just one attempt) only after they have paired. Third, some pelicans display communally, male to male and male to female, on land or water, with flight circuiting interspersed. Eventually, pairs form and move off to select a breeding site, apparently chosen by the female. Some pelican species defend this by systematic ritualized display. Tropicbirds are unusual; their initial courtship consists of highly ritualized flight (Sp Acc) which appears to bear no relationship to the actual breeding site.

Territorial behaviour

Overt territorial behaviour relates strongly to the degree of site-competition and site value may be topographical and/or social. If there is little advantage to



2.6 Beak grappling in the brown pelican; fighting in the Atlantic gannet. (Drawings: J.P. Busby.)

site and/or mate fidelity, the optimal procedure is that which requires least investment of energy. Owners can discourage conspecific intrusion simply by site-guarding and direct or ritualized threat. Bill grappling (Figure 2.6(a)) is commonly employed by peleciforms though, according to species, varying in frequency by factors of tens or hundreds. Strenuous, overt fighting, which may cause significant damage, is common only in gannets (Figure 2.6(b)) and (in some localities) tropicbirds.

Sulids have gone much further than the other families in evolving display whose sole function is to proclaim site-ownership; for example, such display sweeps contagiously through nesting gannets throughout the breeding season. Most boobies, too, frequently perform their ownership display, which, in its form, bears no obvious relationship to overt threat.

Cormorants and anHINGIDS show ritualized post-landing behaviour which relates to ownership of the site and is to that extent territorial but then, even early in the season, they quieten down and do not thereafter repeatedly perform a specific site-ownership display. Nor do any of the pelicans. In both of these groups most site-associated behaviour

is associated, also, with the partner's presence and is thus difficult to disentangle from the pair relationship, whereas in sulids even males landing on empty sites perform ownership displays and may continue to do so regardless of the lack of intrusion or the presence of the mate. Frigatebirds defend their sexual display sites purely as a response to intimate intrusion and not as a pre-emptive declaration of ownership. Nor, if this site does become the breeding site do they even then defend it by such a display but simply by grappling and threat. This stems from their habit of moving their sexual display site from place to place. Each time a male moves to a new display position he must be ready to firm-up his attachment to that site if he acquires a female, otherwise he must move elsewhere. In evolutionary terms it would be difficult suddenly to change the entire stimulus-response system and begin to defend by ritualized display a site which, a few hours ago, had he not acquired a female, he might have abandoned altogether.

In flight-circling, a form of territorial behaviour common to pelicans, sulids and cormorants, the male flies round and lands again, with calling and post-landing display. This continues during

pair formation, but its occurrence before the pair-bond has formed marks it as territorial behaviour.

Pair interactions

Pairs form when females respond to special, often complex, 'advertising' displays by males. In pelicans, sulids, cormorants and anhingids these ritualized displays derive from a common source—they are homologous and the similarities are obvious (see figures at end of Chapter 5). Head-shaking, bill-tucking, wing-lifting, neck-lengthening, head-feather raising and displacement nest-building often follow the advertising display. Further pair interactions involve ritualized locomotion and the behaviours which precede and follow it. Sulids and some cormorants excel in the variety of these components and their use as continuous behavioural dialogue expressing shifting motivation. The alteration of the facial region by depressing or spreading the tongue bone is characteristic of cormorants, anhingids and Abbott's booby but not of other sulids or of pelicans. The face and head are focal points of display in seabirds and boobies, anhingids, cormorants and pelicans have evolved striking head adornments.

Gregariousness may have facilitated the communal pair-formation display that occurs in frigatebirds, pelicans and tropicbirds. Even in some cormorants a group within a colony may display simultaneously to a prospecting female, but unlike the comparable situation in frigatebirds, each male is on its presumptive site and will not move from group to group (for a possible function of the unusual behaviour of frigatebirds, see great frigatebird Sp Acc).

The communal pairing of ground-nesting pelicans (GFA) is unique within the Order, although the male-male interactions that occur within displaying groups remain to be interpreted. Some pelicans, particularly the arboreal brown and pink-backed show more 'normal' behaviour in which the male selects a territory and advertises from it.

Tropicbirds seem aberrant. Their communal aerial display seems sexual rather than territorial but the details of mate choice remain obscure. Conceivably, but perhaps improbably, potential mates may assess

physical state and performance during prolonged flight interactions.

The fundamental peleciform pair relationship is serial monogamy; none are known to be polygamous with the partial exception of the magnificent frigatebird, flightless cormorant and perhaps blue-footed booby (Sp Acc). Surprisingly, cooperative breeding is unknown. Cooperative breeders—'helpers' feeding young to which they are related as in the desert babbler (*Turdoides squamians*), Wittenberger 1981—benefit from enhanced food-collecting potential in impoverished land habitats, comparable to the equivalent in tropical seabirds. Of all peleciforms, 80–90 per cent are likely to change partners with each breeding attempt, though some may retain mates for two or three successive breedings. Only gannets and Abbott's booby within the entire Order are known to show high mate fidelity and in fact these are the only species which show highly ritualized, season-long greeting ceremonies. It would be impracticable to quantify the complexity of pair-bonding behaviour but it may be noted that pelicans and frigatebirds have little or no ritualized meeting behaviour whereas cormorants, anhingids and particularly sulids do and it is in the latter groups that pair-bonds last the longest. Tropicbird partners perform intimate though not highly ritualized pair-bonding behaviour and their bonds often endure. However, more widely, there are anomalies. Geese continually and ecstatically reinforce their bond, which duly persists, whilst raptors do not yet still maintain long-term bonds.

Perhaps in part due to their internal, food-carrying method, peleciforms lack courtship feeding. Most of them will not recover spilt food and transfer would have to be bill-to-bill.

Pair formation is to be distinguished from pair maintenance. However short the bond, it has first to be formed and sexual-advertising behaviour is as well developed in species which regularly change mates as in long-term pairs. In peleciforms (except tropicbirds) male advertising is perhaps more strongly developed than in any other seabirds except penguins. One recalls the exotic advertising display of frigatebirds, the bizarre wing-flicking and throwback of cormorants and anhingids, and the

contorted wing-swivelling of boobies (Figure 2.7). On the other hand, the gannets have inconspicuous advertising but highly developed pair-bonding display (see figures at end of Chapter 5).

No pelecaniform is known to maintain contact between partners away from the breeding colony and, as mentioned, pair-bonds are generally short-lived. Yet permanent bonding has advantages such as effective cooperation in breeding. Individuals that approach the breeding season already paired gain over those that start from scratch, and species with long reproductive lives stand to gain most from mate fidelity and the perfecting of reproductive behaviour. Acting against permanent bonding is: the difficulty of precise synchronization of reproductive condition in an a-seasonal environment; difficulty in reacquiring the previous site to act as a meeting point; and the possibility that non-breeding years,

which occur in many long-lived seabirds, may not coincide in male and female. It is unconvincing to suggest that divorce is an upward progression to a better quality mate, though getting rid of incompatibility would be advantageous and probably does occur in many seabirds. For example, gannets and kittiwakes are more likely to change partners after unsuccessful breeding. Catry *et al.* (1997) provide a useful discussion of 'incompatibility' and 'upward progression' in the great skua; Coulson (1966) and Coulson and Thomas (1985) for kittiwakes, and Mills (1973) for red-billed gulls, provide details of the benefits of mate compatibility.

Copulation

Copulation usually occurs on the nest site. In pelecaniforms, unlike gulls for example, each mating



2.7 Pair-formation may involve ritualised 'advertising' by the male, as here in the Peruvian booby (male on left).

consists of a single cloacal application and, except for gannets, lasts fewer than 10 seconds. It may be repeated several times an hour and typically commences at least two weeks and in some species two months before the egg is laid. In the latter case it serves a social rather than a purely fertilizing function. Pelicans and frigatebirds may lay little more than a week after pair formation, about the time from shedding the ovum from the follicle to completion of the shell (Grau 1984).

For most peleciforms little is known about extra-pair copulations (but see European shag). It seems they are not common, yet there have been surprises in this area (Graves *et al.* 1993b). Early in the peleciform pair relationship pairs spend time together on the nest, though this is likely to be concerned with guarding the nest or site and perhaps with pair-bonding rather than mate-guarding.

Behaviour associated with nest, egg and chick

Nest-building

Whilst tropicbirds and some sulids make the merest of scrapes, frigatebirds construct a flimsy twig platform and some cormorants, gannets, pelicans and Abbott's booby may establish huge, solid structures. These differences are to do with energetics; each species does no more than it needs. For frigates it is difficult, expensive and sometimes dangerous to garner nest material, and the chick's prehensile feet enable it to cling securely to the small guano-cemented platform or underlying twigs. There is no danger of water or mud accumulating and chilling the small chick, as there is in some ground-nesting peleciforms which therefore make a solid pedestal. Tropicbirds do not need a nest. Tree-nesting pelicans, cormorants and anhingids with broods of two, three or four chicks with non-prehensile feet build substantial nests. Some sulids, cormorants and pelicans make their nests entirely from excreta, reflecting the scarcity of other material and/or as an adaptation to cliff-ledge nesting. Throughout the Order, males gather most or all of the nest material, an activity which in all cases, and probably primitively, is associated with copulation

and other pair-bonding interactions. Both sexes, or in many species mainly the female but never mainly the male, build the nest. Nest or ground-touching, a common displacement activity in all peleciforms, is incorporated into pair-interactions.

Incubation

Sulids incubate eggs under webs whilst pelicans, cormorants, and anhingids incubate them on top. Frigatebirds and tropicbirds are often (wrongly) said to possess a single, median brood-patch. Their webs are small, or vestigial (frigatebirds) and useless as a substitute for a brood-patch, and the egg receives enough heat through the abdominal feathers. In all peleciforms both sexes incubate though not always equally (Sp Acc). With the notable exception of some sulids, nest-relief on eggs is perfunctory, without prolonged ceremony.

Care of young

With important exceptions, such as the magnificent frigatebird (and, to a lesser extent, other frigatebirds), flightless cormorant, and possibly some populations of the blue-footed booby, peleciform sexes divide care of young about equally. The exceptions largely concern female-centred care of post-fledged young and relate to sex differences in breeding frequency in that the male begins a new cycle with another female. Early care consists of close brooding and feeding, but once the chick can regulate its own temperature (which varies with family from one or two days to two weeks or more) most peleciforms simply guard them and cover them at night. The ecology of each species differs and dictates the time allocated to brooding or guarding young which, with feeding frequency, varies in adaptive ways.

No peleciform carries food exposed in its bill. Presumably depending on the distance it is transported, food may be carried higher or lower in the alimentary tract and may thus reach the young fresh or partly digested. The extent to which digestion can be inhibited during transport may be variable. Apart from tropicbirds, (Figure 2.10(b)) all peleciforms feed their young by incomplete regurgitation (Figures 2.8, 2.9 and 2.10(a)) (or, in some species, in the early stages, by complete regurgitation) rather



2.8 The pelecaniform method of feeding young is by incomplete regurgitation as here in the great frigatebird.

than presenting it or placing it in the chick's gape. Taking food directly from the parent's throat places severe demands on hatchlings, which are weak, uncoordinated and exceptionally small in relation to adults (in extreme cases little more than 0.5 per cent of adult weight).

Alone within the Order, and for unexplained advantage or evolutionary reason, ground-nesting pelicans may handle their young extremely violently as a prelude to feeding them.

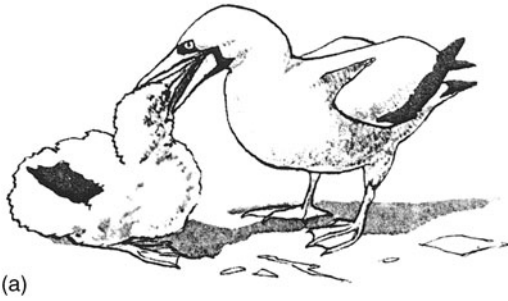
Pelicans and some cormorants, but apparently not other families, may transport water (in their crop?) to their young. In addition to regurgitating it into the chick's gape, the parent pours some onto its

back, presumably to cool it, though possibly by accident. Anhingas are said, in hot weather, to wet their plumage and shake water over the chicks, though the evidence is fragmentary and anecdotal.

The duration of the dependency period varies hugely between families. Those which develop most quickly tend also to have the shortest post-fledging dependency, reflecting the fact that development is a continuum from the incubation period during which the embryo develops, to the fully independent offspring. Pelicans, cormorants and especially anhingids, which usually feed nearer to the colony than the others, grow the most rapidly. Pelicans produce biomass more quickly than any



2.9 Ritualised begging and feeding in the red-footed booby. (From Nelson 1978b, drawings: J.P. Busby.)



(a)



(b)

2.10 Two methods of transferring food, adult to chick, in pelecaniforms. Tropicbird adult places its bill into that of the chick. In the other families the chick takes food from the parent's throat. (From Nelson 1980, drawings: J.P. Busby.)

other pelecaniform and mostly do not feed their fully fledged young at all. Cormorants and anhingids do so but for considerably shorter periods (usually around a month) than most boobies (up to several months). Frigatebirds, which have the longest incubation and growth periods have the longest post-fledging dependency of any seabird (6–12 months). Once they have flown from the nest site, young tropicbirds, whose initial flight has to be sustainable, almost certainly do not return and may well receive no post-fledging support. Post-fledging feeding is an important variable which can be adjusted at the dictate of economic circumstances. It increases the survival chances of the offspring during this critical period, when mortality is high, but places further demands on the adults and considerably lengthens the breeding cycle, with important consequences for the relationship of breeding to seasonal climatic change and for lifetime breeding frequency. The only sulids to lack post-fledging feeding entirely are the three gannets (see, especially, Atlantic gannet).

Behaviour of young

Brood reduction

Properly mentioned here since it is behaviour shown entirely by the young, without adult participation. The reduction of brood size from the original clutch size is almost universal among polyparous pelecaniforms. Cormorants and anhingids achieve this through 'ordinary' sibling competition for food during various stages of chick growth. Survivors are mostly from first and second eggs, in this resembling other groups such as raptors, corvids and herons. In some boobies and pelicans, however, reduction is the consequence of systematic and persistent attack by the first-hatched upon its sibling and at that point has nothing whatever to do with simple competition for food. Indeed, it sometimes occurs even before the second chick has fully emerged from the egg.

The young pelecaniform's feeding and begging behaviour varies with species. Small chicks have great difficulty in extracting food from their parent's bill or throat—a procedure which is much more difficult than having fragments placed into their open mouths as in raptors and may be responsible for many chick deaths in the first day or two. Incomplete regurgitation is a likely concomitant of the adult's method of carrying food internally. The only pelecaniforms which do not use it (tropicbirds) are also the only ones with active hatchlings capable of well-coordinated movement. Yet these are the only chicks that *could* easily take food directly from the throat! Begging is accompanied by vocalization and parents may recognize their offspring's voice, though experimental proof is usually lacking and some species, for example Atlantic gannet and red-footed booby, readily accept substituted young. Atlantic gannet chicks appear to recognize the calls of incoming parents but this inflying-vocalization is an integral part of site-establishment and has not evolved especially for communicating with young. The large young of most boobies and cormorants and all pelicans often beg frenziedly, sometimes severely discomfiting the parent (Sp Acc), but those of the cliff-nesting Atlantic gannet and the canopy-nesting Abbott's booby, to name but two, are notably restrained, presumably related to the danger of falling.

Uniquely, young pelicans may fall into convulsions and coma after, or sometimes before, feeding.

Crèching

Within the Order, crèching in its most extreme form is confined to pelicans, where it may be thermoregulatory, anti-predator and defence against conspecific adult interference. It is found in some cormorants but their crèches are usually looser and less organized (but see Brandt's cormorant). Crèching occurs only in species which will feed their young away from the nest site (some, such as Abbott's booby, will not do so). Even after fledging, pelicans will feed young at the edge of a crèche.

Ontogeny of behaviours

Play, prey-handling movements, handling nest-material, nest-building, body care and, in boobies, cormorants, anhingids and pelicans, fairly complete versions of ritualized territorial and sexual display, develop in a predictable sequence (Sp Acc) whilst the young are still partly downy. Interactions between young birds may help to polish basically innate responses, thus facilitating subsequent adult communication behaviour. Many seabirds and raptors, with skilled hunting and prey-handling behaviour, 'practise', using inanimate objects such as twigs. It seems that motor patterns involved in prey-catching develop within the neuromuscular system during the period of pre- and post-fledging parental care. Even after complete independence, fish-catching skills continue to improve (e.g. Dunn 1972). Nevertheless, many newly independent young die.

Fledging

This term is ambiguous and to make sense depends on context. For a seabird it cannot always mean simply leaving the nest, for gulls, terns and some auks may do so as small, fully dependent chicks and the latter even go to sea. Nor can it mean simply independence from parents since many seabirds remain fully dependent long after they have left the nest, can fly, have begun to feed themselves and thus have 'fledged' in several senses. Usually, and certainly for pelecaniforms, fledging means becoming

capable of sustained flight (or, in the flightless cormorant, swimming and diving).

The well-grown young of ground-nesting cormorants, anhingids, pelicans and boobies practise flying before they achieve full flight, thus blurring the point at which fledging occurs. Tree-canopy and sheer-cliff nesters must fly adequately first time, as, also, must tropicbirds and frigatebirds because of their awkwardness on land and (frigatebirds) on the sea. Whilst post-fledging feeding is usually either fully present or absent in a species, it varies in length, to the point that individuals of some pelican species receive it whilst others do not, presumably because they cease to beg. Conjecturally, the nutritional state of the juvenile may be the determinant.

No pelecaniform is known to accompany its offspring on dispersal or migration, as do some terns, nor to feed it at sea. However, some cormorants will feed their offspring on the water or sea-rocks near to the colony whilst anhingids do so on branches away from the nest. Frigatebirds and boobies feed theirs only on the nesting territory and Abbott's booby only on the precise nest-site even if there is no nest.

Movements

Pelecaniforms show everything from true migration—a shift in the centre of population from A to B and back again—to complete sedentariness. In between there is extensive uni- or multi-directional dispersal, local dispersion, variability between populations of the same species and, even within a population, differences relating to age class.

The difference between juvenile and adult pelecaniforms in migration/dispersal is most marked in the gannets in which juveniles predictably move 4,000–6,000 km to known wintering areas, but in general juveniles migrate or disperse further than adults during the often extensive period before attempting to breed for the first time.

Migration and dispersal: (a) avoids inhospitable conditions such as freeze-ups (Russian populations of the great white pelican) or frequent gales and turbulent seas (some Atlantic gannet populations, where juveniles are particularly vulnerable) or drought (some interior continental cormorants and pelicans); (b) enormously enlarges the foraging area, releasing birds from the constraint of return to

a fixed base; (c) facilitates finding and remaining in the vicinity of food; (d) may reduce the level of competition for food; (e) for inexperienced juveniles migration may provide access to a more favourable prey spectrum and/or density, under more propitious conditions than in home waters.

Many of these advantages seem particularly important in impoverished marine areas, which is probably why almost all tropical, pelagic pelecaniforms are nomadic between breeding cycles. Strong counter-vailing selection pressures, such as the need to maintain a presence at the breeding location, or where dispersal is impracticable, lead to exceptions.

Pelicans

Vary widely; some which breed in strongly seasonal climes migrate. The great white is resident or dispersive south of the Sahara but northern populations, either partly or entirely, are truly migratory. In the American white even the same population contains both resident and migratory individuals. The closely related Australian pelican is resident or dispersive rather than migratory. Some populations of brown pelicans disperse coastally, though a more definite population-shift from A to B and back again also occurs. In pelicans, wider dispersals may be superimposed on more local ones and on feeding movements, leading to complicated patterns. This appears to characterize the post-breeding behaviour of the entire Order.

Gannets/boobies

True migration occurs in the juveniles of the three gannets, but not thereafter. Boobies merely disperse to variable extents. Red-footed, masked and brown boobies have been recorded thousands of kilometres from their breeding area but their movements appear to be nomadic rather than strongly directional. Abbott's booby (unless still breeding) disappears from Christmas Island during the monsoons; it may tend to move NW rather than randomly but is seldom recorded at sea. Under normal conditions the most sedentary adult sulids are the Peruvian booby and some populations of the blue-footed and brown boobies. Indeed, some brown boobies, as on

Ascension, appear to remain on their territories year-round.

Cormorant/shags

Represent every gradation of dispersal from extremely local to widespread, from dispersal in many directions to population-specific tendencies to move in one direction, from annual dispersals to occasional, food-related eruptions. They do not normally attempt long sea crossings but their opportunistic nomadism is the land-based equivalent of the pelagic nomadism of truly marine pelecaniforms and, like it, confers great advantages in locating food sources and saving energy in travel. Nevertheless, true sedentariness is found in some cormorants, though mainly in the island-endemics of the sub-Antarctic. But many individuals even of more widespread species, such as the European shag, are sedentary.

Anhinga/darter

The anhinga and darter are largely resident but may move a few hundred kilometres away from the breeding area.

Frigatebirds

Those which are not still feeding dependents may move far. Even the endemic Christmas frigatebird has been recorded thousands of kilometres away from Christmas Island, whilst some great and lesser frigatebirds wander widely between islands and thousands of kilometres further afield. The dearth of islands within the Atlantic region of Ascension Island may inhibit extensive nomadism in the Ascension frigatebird which, like its congeners, is thought to be incapable of roosting on the sea because its plumage is not waterproof.

Tropicbirds

All three, though with variation between populations and individuals, are far-flung pelagic wanderers, probably remaining unbrokenly at sea for longer than any other pelecaniform. But they are not known to be strictly migratory.

Breeding ecology

Introduction

This chapter concerns some major aspects of peleciform breeding biology such as coloniality, timing and frequency of breeding, clutch and brood size, chick growth, and breeding success. The diversity of the *Pelecaniformes* affords particular insight into inter-related aspects of seabird breeding biology such as the adaptive web based on feeding and foraging regimes.

Some cormorants and pelicans breed outwith the marine environment altogether, in the interiors of continents from sea-level to hundreds of metres above it, a range of habitats unmatched by any other seabird taxon. Pelecaniforms have adapted to most breeding habitats including flat ground, cliffs and slopes, trees, bushes and other vegetation. However, only tropicbirds and one or two shags nest in cavities and none in self-dug burrows, though tropicbirds will enlarge natural holes. Representatives of all five families utilize trees or bushes, possibly due to pressure on nesting habitat in the evolutionary past. No peleciform is mainly nocturnal, as are some petrels and shearwaters, so, unlike them, none has evolved nocturnal flights involved in courtship or the use of olfactory cues.

Colonial breeding

General aspects

A typical seabird colony is a breeding aggregation in which individuals are almost constantly exposed to the stimulus of conspecifics. Usually there is competition for territory and mate, and strong

adherence to the group. Many colonial species feed and gather nest material communally. Unlike many landbirds, seabirds feed outside their territory which is often merely the nest site. Almost always, within a colony or sub-colony, breeding is markedly synchronous. Although most seabird colonies persist for years, sometimes centuries, in the same general location—an island or a stretch of mainland cliffs—the individual may, according to species, show everything from strong fidelity to the precise nest-site, variable movement within a colony, to change of colony. Indeed, in most peleciforms, some movement during a lifetime is far commoner than fidelity to a precise site.

The colonial habit grades into dispersed or solitary breeding and the difference between a colony and a sub-colony defies sensible definition. This is more than semantics; ideas about population dynamics, resource-depletion and interaction between colonies presuppose that 'a' colony can be defined. For example, the average emigration rate of shags ringed as chicks was 22.5 per cent from an island in the Firth of Forth but only 1.5 per cent from the Farnes. But when the south Forth group of islands was counted as a single colony, disregarding exchanges between neighbouring islands, the emigration rate was only 2.2 per cent, similar to the Farnes (Aebischer 1995). So can 'a' colony always be precisely demarcated? What determines an individual's choice of colony? Natal philopatry, current spacing in the colony and the colony's behavioural profile may all be involved. What is the social structure (age, status and experience) within an apparently homogeneous group? What is

the nature of competition for space and a mate within a colony? Do individuals constantly strive to improve the quality of these? Is there a relationship between colony size and productivity? Do colonies of the same or different species compete for food? How do colonies begin and what are the dynamics of growth? Why is breeding in large colonies so characteristic of seabirds? Few of these questions have been answered.

Colonial breeding involves costs and benefits. Enhanced defence is paid for by increased conspicuousness, help in locating food may mean increased competition for it, facilitated pair-formation means competition for a mate. But these are impossible to quantify.

Most peleceniforms are colonial. Only Abbott's booby, two or three cliff-nesting shags, and some tropicbirds may habitually nest out of sight of conspecifics, though they still come into regular contact with them. At the other extreme, guanay cormorants and African gannets are among the densest of all seabirds. Colonial breeding has arisen in several avian lines and is considered to be an advanced social system; helpful reviews are in Gochfield (1980); Wittenberger and Hunt (1985); Kharitonov and Siegel-Causey (1988); Siegel-Causey and Kharitonov (1990). Three factors seem paramount in predisposing seabirds to breed in colonies: adequate food within the foraging range; shortage of breeding sites; and (though rarely applicable to peleceniforms) defence against predators.

Colonies and food (Figure 3.1)

Whilst abundant local food sustains large concentrations of seabirds (Humboldt, Benguela and Californian currents) colonies of tropical pelagic seabirds may be huge even though surrounding seas may contain only patchy and unpredictable food (but growth of six tropical pelagic species during a period encompassing a major ENSO, suggested food is not unpredictable—Shea and Ricklefs 1996); indeed, tropical pelagic and migratory seabirds are more numerous and breed in larger colonies than local, sedentary foragers. Even within the same species, colony size increases with available foraging area

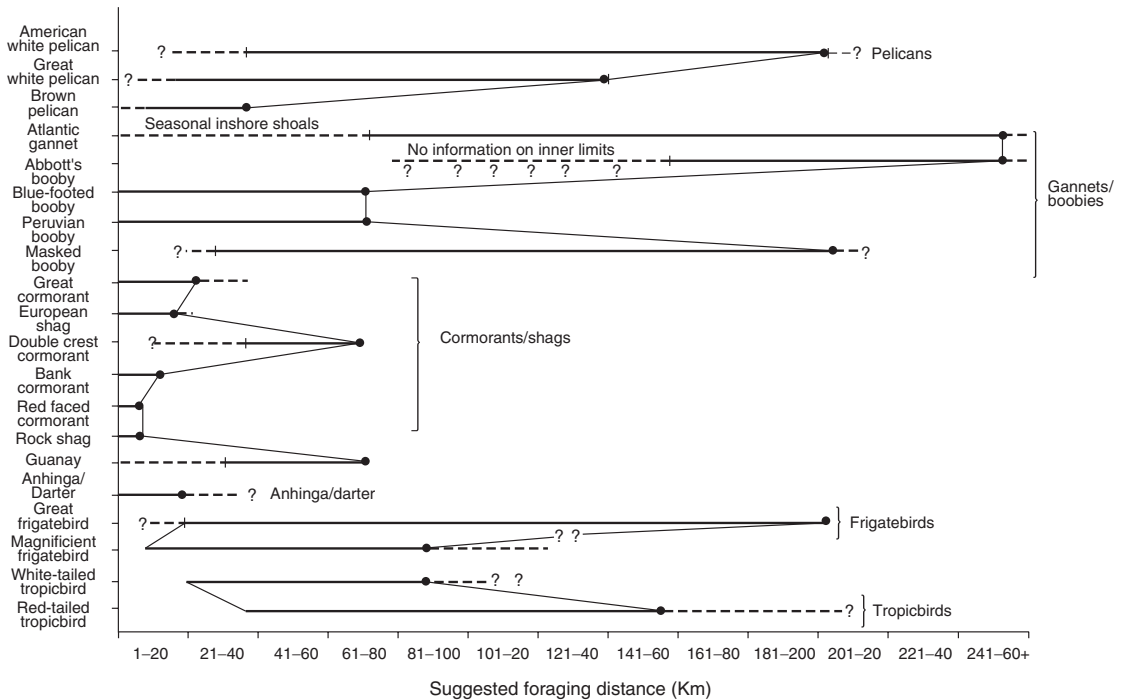
(Birkhead and Furness 1985). Smaller colonies are often typical of species which feed solitarily or in small groups on more uniformly and thinly distributed resources, or of species with very restricted foraging ranges such as some cormorants, most obviously the flightless. Among terns, the pelagic sooty tern forms huge colonies whereas those of inshore feeders, such as black-naped, common and Arctic terns, are smaller. Correspondingly, the latter feed their young more frequently, lay clutches of more than one egg compared with the single egg of the sooty, and their chicks grow more rapidly (Hulsman and Smith 1988).

Horn's (1970) 'geometrical' model has been widely cited as showing that the average distance that a bird must travel to find food is least for birds nesting in the centre of the foraging area. If large numbers do so, colonies will ensue. However Wittenberger and Hunt (1985) show that this model rests on assumptions which may not be valid in real life. For instance, it assumes that the colony is located 'within' the foraging area; that each bird forages with equal frequency at every point in the area during the breeding season, which seabirds do not, and that the prey is unpredictable in space and time, which often it is not.

Where food is patchy, 'network foraging', spread out over an area, can be an advantage. Successful birds then attract conspecifics and prey in that area may be temporarily abundant enough, perhaps at a local upwelling or current boundary, or in shoals, as of herring or mackerel, to offset any feeding competition. Indeed it is probable that each individual can be more successful when fishing in a flock than singly since repeatedly startled fish become slow once their fast-swim mechanism has been exhausted (Schmidt-Nielsen 1975). As Darwin noted, diving gannets attract others from afar, which is perhaps one function of their dazzling plumage. Colonial breeding could enhance network foraging if, without it, the density of birds would be too low to search the area thoroughly. On the other hand it might militate against uniform searching.

For seabirds it seems highly unlikely, except in the most general way, that colonial nesting transfers

38 Pelicans, Cormorants and their relatives



3.1 Foraging ranges of pelecaniforms.

information about the location of food. Skeins of gannets arriving at the Bass Rock from the south indicate that they have been feeding there, but since there is a traditional fishing area off the Farne Islands such information is of limited import. Wittenberger and Hunt (1985) suggest that information transfer of a more specific nature could operate only if food is patchy (it often is), patches endure long enough for birds to reach them (often they would not), previously successful individuals who are returning to the area in which they had been successful can be recognized as such by departing foragers who can therefore follow them, and finally such followers are more successful than other foragers. There is little or no evidence for any of this.

In theory food could determine the location and size of seabird colonies. If there was insufficient, nestlings would starve and numbers would become appropriately adjusted (Ashmole's 1963 density-dependent mechanism). Seabirds could significantly

depress fish stocks (Furness 1982) and thus affect the number and size of colonies within their common feeding area (Furness and Birkhead 1984). And due to enhanced competition for food, large seabird colonies could be less productive per pair than small ones (Gaston *et al.* 1983; Hunt *et al.* 1986). The depletion of food around concentrations of breeding seabirds has been demonstrated for two large colonies of double-crested cormorants (Birt-Friesen *et al.* 1987), but for obvious reasons it has not been demonstrated for any pelagic, far-foraging seabird.

Ainley *et al.* (1990), for six seabirds nesting in large numbers on the Farallon Islands 40 km off California, showed that within the 3,200 km² in which they feed much of the annual variation in reproductive success could be explained by perturbations in the marine food web. These were much more complex than generally appreciated. ENSO appears to be only one of the global atmosphere-ocean phenomena affecting the

California current which may produce good years as well as bad. Thus, estimating the relationship between colonies and food can be dauntingly difficult. Wilson (1991) conducted a comprehensive examination of the relationship between sea surface-temperature anomalies and the annual numbers of nests of double-crested and Brandt's cormorants on the outer coast of Washington's Olympic Peninsula but could only tentatively conclude that there were fewer cormorants when the sea was warmer.

Furness and Birkhead (1984) computed that *large* colonies of gannets, puffins, shags and kittiwakes had only *small* colonies within their common foraging range. They concluded that birds from adjacent colonies compete for food. Thus birds from a large colony may limit the size of neighbouring colonies by depleting resources. However, Cairns (1989) based on Diamond (1978) proposed that 'seabirds from neighbouring colonies typically occupy non-overlapping feeding zones' and that colony size is related to the extent of the foraging area used by the colony. He suggests that birds should not feed nearer to other colonies than to their own because if they did so they should, for economy's sake, nest at the closer colony provided that sites are available. He calls the feeding area around a colony which is closer to that colony than to any other the 'hinterland'. Despite its common-sense appeal, this model encounters practical snags. Feeding areas often *do* overlap, food moves around, nest sites may *not* be available close enough to the best feeding areas, and, most importantly, relative densities of food at different distances from the colony will affect the economics of foraging distance. Nevertheless, feeding areas specific to particular groups of closely adjacent blue-eyed shags breeding on South Georgia have apparently been demonstrated (Wanless and Harris 1993) and mutually exclusive feeding areas may be much commoner than general observations suggest. Even from large colonies, such as the Bass gannetry, it may be that individuals persistently fish in specific localities.

Chicks of the kittiwake, common and Brunnich's guillemot and red-faced cormorant from a small colony grew faster and were heavier at fledg-

ing than those from very large ones (Hunt *et al.* 1986). But direct measurements of depletion of food as a function of colony size are not available for any seabird though circumstantial evidence includes the observation that after a massive cull of adult herring gulls on the May (Scotland), the body weight of birds breeding for the first time rose, and eggs increased in size (Parsons 1976), suggesting an improvement in food. This says little about genuine seabirds since herring gulls feed much on land and at artificial sources at which younger birds are sub-dominant (personal observation).

Colonies and breeding habitat

Although pressure on habitat can be acute it does not nowadays usually control seabird numbers. Man has exterminated entire populations and species (e.g. Steadman 1989) and present numbers may well be a fraction of prehistoric ones, though exceptions to this have resulted from the relatively recent huge amount of discards from fishing fleets. More than any other seabirds except gulls and terns, peleciforms breed in virtually all types of habitat, although due to extreme morphological specialization evolved for foraging, frigatebirds and tropicbirds are least versatile. This adaptive radiation may have been encouraged by competition from other seabirds. For example, tropical pelagic seabirds exist in huge numbers because they are able to exploit vast feeding areas and if, as it often is, breeding habitat in oceanic tracts is scarce, colonies will be large and adaptive radiation into all available habitats will be encouraged. This may account for white-tailed tropicbirds nesting (dangerously) in trees far inland on Christmas Island (IO) or in the Waimea Canyon (Hawaii) (personal observation).

Where closely related species use the same area and habitat they segregate, as, for example, great and lesser frigatebirds in the mangroves of Aldabra or brown and masked boobies on the bare slopes of Bosunbird Island (Ascension). A possible generalized explanation for segregation is that it minimizes competition for breeding space, but critical evaluation is never available. Indeed the facts may be

awkward; the commonest frigatebirds, the great and lesser, are the two that overlap the most both in distribution and habitat; moreover, they take similar prey (Diamond 1975a).

Seabirds usually nest more densely than available space would dictate, even when site requirements are specialized and when suitable unused ones (critically evaluated) are shown to exist within the colony (Olsthorn and Nelson 1990). Similarly, Siegel-Causey and Hunt (1986) demonstrated for the double-crested and pelagic cormorants that inferior sites were settled on *before* all the best ones had been taken up. Empirical observation suggests the same for many seabirds.

In general, I suggest that limitation of the number of breeders or the imposition of excessive density, as in the vast and crowded colonies of the Peruvian guano islands, because of shortage of sites, is the exception.

Density and size of colonies

The species-typical density at which different seabirds breed is not understood. The structure of a colony involves the social attributes of the nest site (such as central or peripheral) and the age, experience, physical attributes and behaviour of the owners. Since Coulson's (1968) study on the kittiwake, central sites are considered to be superior to edge ones and to be occupied by better quality individuals, but his colony (on the window ledges of a disused warehouse) had some peculiar characteristics which could vitiate general conclusions. The edges of undisturbed gannet colonies are *not* more prone to predation than more central sites except that, if the colony is expanding, the younger birds that occupy them tend to be less efficient incubators and may 'voluntarily' leave eggs untended. Their lower breeding success is certainly not due to inferior sites.

Whether or not centre-site peleciforms are better-quality birds, in most species more than 90 per cent of the breeders cannot sensibly be classified as 'edge' or 'centre' and in changing populations both categories may soon lose that status. The novel proposition which Ens (1992) derived from his studies on oystercatchers—that more than 90 per

cent of birds are mated to 'sub-maximal' partners and/or occupy sub-optimal sites and are constantly striving to better their lot by contesting other sites and by stealing mates—is altogether contrary to the evidence in those (many) long-lived seabirds which are strongly faithful to mate and site.

Since peleciforms adhere to socially imposed, species-typical spacing within colonies this must be an evolved trait brought about by natural selection. Yet the factors which have produced the dispersion remain obscure except for those species which, due to shortage of habitat, nest as densely as physically possible. The simplest unifying hypothesis might be that, in the past, pressure on space encouraged dense nesting with due regard to contrary pressures such as landing space, room for adults plus brood, cover for young to shelter and adequate display space. Frigatebirds exemplify spacing engendered by social factors.

There are no strong social pressures controlling the *size* of colonies within narrow limits and, unlike species-typical density, colony size varies enormously. The largest peleciform colonies occur either in areas of superabundant food, such as major upwellings, or on oceanic islands subtending vast foraging areas. The colonies of Peruvian guano birds contained literally millions, all of which feed comparatively near to the breeding area. By contrast, some colonies of pelagic tropical boobies and frigatebirds number(ed) scores of thousands whilst sooty tern colonies held millions. But all peleciforms, however large their major colonies, can breed successfully in tiny ones or even, in many cases, solitarily. Yet, large or small, colonies show approximately the spacing typical for the species.

A possible factor in the gross disparity between the consistent species-typical *density* as against the highly variable *size* of colonies is that the former is unrelated to food resources and is thus freed from a major variable which greatly affects the latter. Thus social factors can exert their full effect in determining density.

Sub-groups within colonies

'Sub-grouping' occurs in most colonial seabirds regardless of habitat and with little relation to

density (Nelson 1970). Even in uniform surroundings, as in the sweep of a gannetry, groups are recognizable by conspicuous synchrony in chick age, contrasting with the age in adjacent groups. Sub-groups may result from same-age birds or those which are at a similar reproductive and thus behavioural stage, attracting peers. After a few years, provided site-fidelity is strong, such group boundaries disappear and the colony becomes more homogeneous or local topography may demarcate 'nuclei' around which groups develop. In the colony of blue-footed boobies on the boulder-strewn Punta Suarez of Hood, Galapagos, groups were physically separated and differed in the age of their chicks (Nelson 1978b). In the relatively a-seasonal equatorial environment laying can occur in any month; a few reproductively ready pairs group together and may be separated by days or weeks from the next such group. Even in the plate-flat bottom of Daphne Island crater, sub-group synchrony was evident in the blue-foot. In a temperate seasonal breeder such as the great cormorant, groups along a short stretch of cliff may be markedly out of synchrony with each other but synchronized within each group (personal observation).

Possible functions of this widespread phenomenon include facilitation of pair-formation, inhibition of interference by neighbours and intruders, and a spread of the risks of environmentally-induced breeding failure. Groups at different stages confer a form of breeding polymorphism. Environmental disaster may then affect only a part of the colony. There has been little critical work on the social factors playing a part in the genesis of spacing within a colony but Burger (1988) has shown that little terns are attracted to larger rather than smaller groups, spaced at 1.5 m rather than 0.5 m, to solitary rather than paired birds, and to plots containing both single birds and pairs rather than to either of these alone. Behaviour as well as static pattern must play an important role. These kinds of effects are to be expected in many seabirds. On the Isle of May (Scotland) spaces created by culling herring gulls caused an influx of young prospectors (Parsons 1976).

Six pelecaniform colonies illustrate the diversity of colonial breeding.

1. The Bass Rock, an ancient gannetry, is small and isolated. A prospecting female can rapidly investigate the entire colony. In practice, some parts of it attract grossly disproportionate numbers of recruits, have a higher incidence of territorial and sexual display, and grow more rapidly than others. Some sections are physically demarcated but thousands nest in an unbroken sweep. There is continuous traffic and display throughout the 32+ weeks of the breeding season even though incubation and chick-care occupy only 19 weeks. This is a 'classical' seabird colony: traditional, separate, with a substantial proportion of non-breeders in attendance, intense social intercourse, and marked social coherence (gannets gather nest material communally, rest on the sea in groups, fish in flocks and return to the colony in skeins). Foraging areas are fairly well defined.
2. In contrast, Abbott's booby is the least colonial pelecaniform. Its total world population of some 2,000 pairs is scattered over 100 km² of jungle-clad Christmas Island where birds may be completely hidden beneath the canopy. Yet this population is still 'a' colony; individuals prospect, see, hear and interact with conspecifics. It is isolated, with non-breeders. Birds return in groups from foraging. Yet mostly the island is quiet until the sonorous clamour of a meeting pair carries far across the jungle. Nest material is gathered singly. Yet there is no qualitative difference between the coloniality of Abbott's booby and that of the Atlantic gannet.
3. The large colony of great frigatebirds on Aldabra coexists with one of lesser frigatebirds. The distribution of birds within the mangroves varies from year to year (perhaps through disturbance). Groups of 10 to 20 nests are separated by empty areas. Unlike a gannetry, the period of social activity, though intense, is limited to pair-formation; there is no territorial or pair display throughout the remainder of the long breeding cycle. There are many non-breeders, some in immature plumage, and

much interference by males, presumably of this category, in the affairs of established pairs. Birds gather nest material, and depart and return from foraging, singly, though they often feed in groups.

4. A colony of great cormorants in southwest Scotland introduces further differences. Some 200–300 pairs divided into several unequally sized groups nest along 2 km of estuarine coast. Within each group some nests almost touch whilst others are widely separated. Territorial and sexual display is comparatively infrequent and lasts for only a fraction of the season. The colony is usually quiet and traffic is restricted to incoming and departing birds. Nest material is gathered communally but fishing is usually solitary, although foragers may return in small skeins. The location of each separate group, its size, and the distribution of nests within it, varies markedly from year to year. This ‘population’ well illustrates the demarcation-of-colonies problem, for a few kilometres further along the coast are two more groups. It would be difficult to define this local population as a single extended colony or as three (or five) separate ones. There is probably interchange between them and perhaps between them and other groups yet further along the Solway.
5. The Lake Shala (Ethiopia) colony of great white pelicans, although ancient and huge (Brown and Urban 1969) may be entirely absent in some years because it requires a massive, fairly local food supply. Breeding is opportunistic, which never occurs in pelecaniforms of temperate latitudes, and the colony is sometimes deserted *en masse*. The pelicans nest densely, on the ground on islands (for inaccessibility). Display is highly communal and restricted to a short period of pair-formation. The young form crèches (only some other pelicans and cormorants do this). Feeding is communal and cooperative and birds move to and from feeding areas in flocks.
6. Finally, the Aldabran colony of white-tailed tropicbirds is a loose assemblage of scattered pairs breeding in a variety of sites and often obscured from neighbours. Many of the nesting sites are

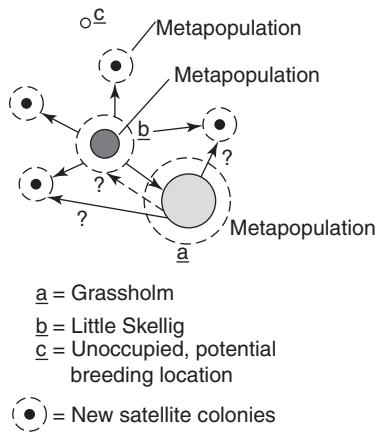
used only intermittently and may remain empty for years (Phillips 1987). Except for pair interactions, social intercourse is exclusively aerial. Nevertheless members are potentially interactive and the colony is geographically discrete. Birds forage often far from the colony and return singly.

Colonies and theory

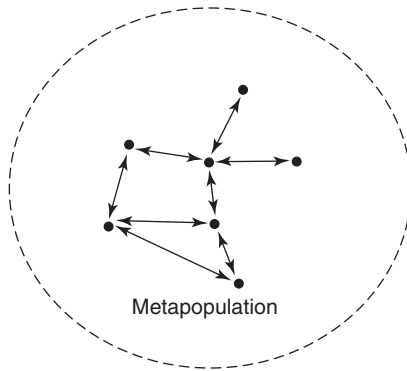
Until recently theoretical approaches to the dynamic features of colonies had considered them as ‘populations-within-populations’, emphasizing that all animals are distributed discontinuously across their ranges. To a variable extent, animals exist as interbreeding sub-populations within a ‘meta-population’. The terminology and modelling of the ‘meta-population’ concept evolved around the dynamics of insect pest populations. Buckley and Downer (1992) applied the idea to seabirds, though Harrison (1991) has cogently argued that the latter may violate so many meta-population principles as to be inappropriate for such treatment. However, if the theoretically fragmented situation regarding the biology of seabird colonies is to be clarified, new approaches are needed.

Buckley and Downer define a meta-population as ‘an interacting cluster of intermittently occupied, discrete sites which exchange breeders’. The word ‘site’ most often applies to the territory defended by a breeding pair so ‘locations’ might be better. And the words ‘intermittently occupied’ are restrictive because many seabirds occupy their colonies every year without fail, or even all year round, which is hardly ‘intermittent’. The meta-population is not necessarily one large colony but may be several colonies either of fairly similar or grossly disparate size, thus providing three major options which could greatly affect the dynamics of the meta-population.

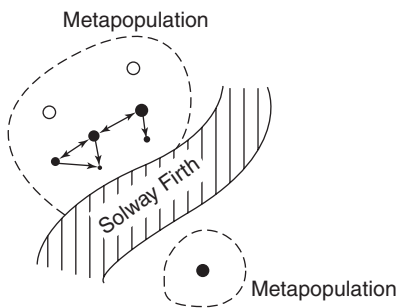
Buckley and Downer apply five of the ten selected ‘types’ of meta-populations to pelecaniforms (Figure 3.2). The configuration which they apply to gannets and which, worldwide, may be the commonest, is inadequate. It depicts (a) a large colony (= meta-population) exporting recruits to several small colonies (each a meta-population)



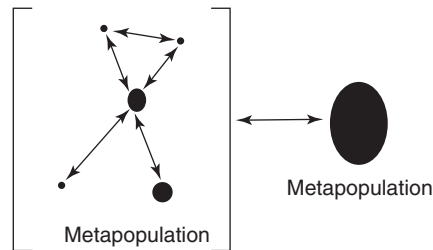
(a) Atlantic gannet



(b) Red-tailed tropicbird (Caribbean)



(c) Great cormorant



(d) Boobies and frigatebirds

3.2 Seabird colonies and theory. (After Buckley and Downer 1992.)

with an unoccupied but potential location for a new colony within range. However, in real life the large colony (say Little Skellig gannetry in Ireland) can export recruits to an even *larger* colony (say Grassholm gannetry in Wales) whilst conceivably some Grassholm-born gannets go to Skellig. Nevertheless, it covers much of the reality. Another model (b) fits the red-tailed tropicbird in the Caribbean where there is interchange between islands but not between the Caribbean meta-population and any other meta-population. With modification it may fit some cormorant populations (c). Another model, they suggest, is applicable to boobies and frigatebirds (d). This is unlikely

to correspond to reality. The idea that small colonies may interchange recruits with each other and with a large colony is correct but there is no evidence whatsoever that a *group* of several small colonies which together form a meta-population would move, as a unit, to a large single colony, nor that the converse could occur.

Buckley and Downer list several special features of seabird biology, some of which apply to the pelecaniforms, and which impinge on aspects of the meta-population idea.

1. Colonies vary asynchronously in size and occupancy. A colony may increase whilst a

nearby one becomes smaller or is abandoned. This applies particularly to some terns which move around *en masse*, one year here, another there. But it can apply to some pelicans and cormorants and perhaps to frigatebirds. It very rarely applies to sulids, although, for example, in Norway a small gannetry declined whilst another, nearby, increased (Barrett and Folkestad 1996). Here, movements of fish prey may have been the cause.

2. Colony size tends not to be uniform nor normally distributed, but rather log-normally. This is obviously true of all pelecaniforms.
3. Adults tend to be long-lived (unlike the insects for which the meta-population concept was coined!).
4. First-year birds suffer heavy mortality, the import of which is that if mortality is even moderately dependent on colony-size one large colony is more vulnerable than several smaller ones.
5. A colony may contain much the same number of breeders from year to year but they may be different individuals. This is an intriguing aspect of colonial breeding. It may conceivably apply to frigatebirds but obviously not to nest-site-faithful species.
6. First-time breeding is often long delayed in seabirds, including pelecaniforms.
7. Experienced breeders may take years-out from breeding.
8. Natal philopatry is common.
9. Members of a breeding colony tend to remain together even when the entire colony moves. This is probably a special adaptation and very unlikely to apply to any pelecaniform, though circumstantial evidence strongly suggests that a group of cormorants may move short distances as a unit (personal observation).
10. Small clutch-size and extended parental care is common.

As many as possible of these daunting variables have to be incorporated into meta-population modelling if it is to have any validity. Buckley and Downer ask, first, which of their 10 life-history parameters most influence population projections;

and, second, how responsive are seabirds (they use an albatross, a cormorant and a tern) to changes in parameters including density-dependence and the distribution of colonies of different sizes. Their modelling suggests that for the cormorant and albatross the most important factor in determining future population trends (*not* the attainment of a particular colony size) is the degree to which mean growth rates of colonies within a meta-population are correlated. If two colonies each have a 10 per cent probability of going extinct and their growth rates are perfectly correlated, then the probability of total extinction is also 10 per cent. But if their growth rates are uncorrelated the probability of their combined extinction drops significantly. Next most important is dispersal (the rate at which recruits from one colony go to another). Then comes the survival rates of sub-adults and lastly the number of colonies (sub-populations).

The model predicts that the single-colony population is at far greater risk than a population of several log-normal or uniform-size colonies. The cormorant single-colony could rapidly become extinct (faster than the albatross) because it is a fairly short-lived species with a highly variable reproductive output. Thus a few bad years in succession could extinguish it. However, if density-dependence is built into the model the benefits of a multi-colony meta-population structure over a single colony disappear.

Clubs and non-breeders

(See GFAs.) The presence in pelecaniform colonies of non-breeders which may gather in so-called 'clubs' or attend the colony without holding a definitive site has been little studied. Mere aggregations of loafing or roosting birds lack the social dimension of clubs. In some gulls, clubs are the focus of pair-formation, where partners meet, court and establish a pair-bond for the current season. In the great skua, clubs are a prominent feature of large colonies; immature and non-breeding birds display and perform some reproductive behaviour within them. There may be many such gatherings on the fringes of breeding groups. Recently founded and growing colonies may include a large club whereas declining ones have



3.3 Part of a gannet 'club', mostly of immature birds.

none. Skuas in clubs are preparing for future bonds rather than establishing bonds for the current season. At a thriving colony many thousands of skuas may pass through the clubs in a season (Klomp 1991).

The Atlantic gannet resembles the skua. There is a similar relationship between colony status and club-size; there may be many birds passing through (some clubs contain thousands); most are immature (from one to four years (Figure 3.3) though there are some mature-plumaged birds of indeterminate age; reproductive behaviour is practised; transitory pair-bonds are formed; eventual nesting may be elsewhere in the colony or possibly in another gannetry altogether. Club gannets gather in large masses or may be dispersed around the colony, perhaps at the edge or on broad ledges among breeders. Apart from their immature plumage, they are behaviourally distinguishable from site-owners. They are less regularly dispersed, move around more, show relatively low-intensity and incomplete territorial and pair-bonding display, are more easily

displaced by other gannets, and are warier. They are clearly less settled and constantly come and go. Nevertheless, where a group is expanding it requires detailed observation to distinguish the outer ranks of birds trying to establish definitive sites, from adjacent 'club' birds, especially at the height of the breeding season, when some slightly immature-plumaged birds are establishing sites for the following year.

At most gannetries, in June and July, there probably is through-traffic of birds which were born elsewhere, especially where several gannetries lie athwart common sea-lanes, as on Britain's western seaboard. In all probability, immature birds from Skellig in Ireland to Hermaness in Shetland bypass, and may visit, several west-coast gannetries. This may allow prospective breeders to assess nesting space and the behavioural profile of a colony—the tempo of prospecting, territorial and sexual display. Also it permits some assessment of the local foraging areas—the location and level of food resources and of intra- and possibly inter-specific competition.

Clubs facilitate social behaviour by 'polishing' the perception of behavioural cues and the expression, in response, of the appropriate motor patterns. Groothuis (1993) has developed this theme for the ritualized behaviour of the black-headed gull and his findings may apply widely.

Clubs are not equally well developed in the six families. Booby clubs are smaller than gannet clubs and less distinguishable from loafing and roosting aggregations. Some cormorants aggregate in clubs in which they form temporary pairs, display, copulate and build 'trial' nests (Kharatinov and Siegel-Causey 1988). Pelicans form roosting and loafing aggregations both away from and sometimes adjacent to breeding groups. In ground-nesting pelicans early in the season there may be precursive activity in such gatherings, leading to the communal display which culminates in pair-formation. Anhingids are not known to congregate in clubs. Tropicbirds appear to lack loafing or roosting aggregations. They may, however, attend the colony and occupy nesting sites without attempting to breed (Stonehouse 1962; Snow 1965; Phillips 1987). Frigatebirds attend roosting and loafing aggregations in and around breeding colonies, but without conspicuous interactions between individuals. Whether the intruder males which cause mortality among nesters are loafers is unclear.

Porter and Coulson (1987) point out that the number of non-breeding kittiwakes at a colony may provide an early warning that something—presumably, usually food—is adverse.

Colonial nesting and philopatry

With notable exceptions, seabirds tend to nest in the colony of their birth (natal philopatry). The developing chick becomes imprinted on its surroundings as shown by the ability of displaced chicks of many ground-nesting species, including some pelicans, cormorants, and sulids, to return to their nest site from a distance. However, this accounts only for recognition of the immediate surroundings; for burrow-nesters which depart at night, hardly even that. Yet few short-tailed shearwater chicks transferred to a new island before fledging returned there, indicating that, by whatever mechanism (smell?,

sound?), they had become aware of their birth island before they were removed (Serventy *et al.* 1989). Brooke (1978a) showed that in the Manx shearwater only 13–14 per cent of young birds were re-trapped away from the precise area from which they had fledged. Among shags born on the Farne Islands, 78 per cent returned precisely to their birth area on either Staple or Brownsman although these are a mere 100 m apart (Potts 1969) but only 42 per cent of red-billed gulls were from their natal colony (Mills 1973), and an estimated 90 per cent of fulmars which survived to breeding age emigrated from their natal colony (Ollason and Dunnet 1983). I have noted a marked tendency for Bass Rock Atlantic gannets, colour-ringed as chicks, to return there—in one case to the ledge from which it fledged. But many return to a different part of the Rock or move further. Two colour-ringed birds settled at Bempton, 240 km south, whilst a chick from Ailsa Craig, Scotland, bred in Norway and an Icelandic one on the Bass. The rate at which some gannetries have grown shows that large-scale immigration occurs (Sp Acc).

The scale of emigration and immigration means that, whatever the adaptive significance of natal philopatry, such as breeding where your parents were successful, or remaining part of a locally adapted population, great advantages may attend emigration. The prevalence of 'prospecting'—individuals rapidly visiting colonies many kilometres apart before settling to breed—suggests that the social attributes of a colony (spacing, age-structure, behaviour) are important (Nelson 1989). 'Pioneering', an extreme form of prospecting, may result in the founding of a new colony or an extension of range, but even the latter does not necessarily indicate that existing colonies are full.

Breeding philopatry

This is when, having once bred, the individual thereafter breeds only at that colony. It applies widely, the pelecaniform exceptions falling among opportunistic breeders, especially some pelicans, and among cormorants.

Some African populations of the great white, and some Australian pelicans, are highly opportunistic

breeders, settling and nesting in different localities when conditions are favourable, or using the same locality but intermittently. Other populations of the great white, Dalmatian and American white may be faithful seasonal breeders within a permanent colony, although the precise sites of individuals change. Colonies of the pink-backed and spot-billed may be extremely traditional and persistent, though again, individual sites may change. Nest-site permanence for a specific pair is unproven for any pelican. Opportunistic breeding seems to be an adaptation to particular, and over the family's range as a whole, unusual conditions.

Breeding philopatry seems total in Atlantic gannets and individual nest sites are typically maintained for life. Young tropical boobies move widely between islands and may breed on non-natal ones, but having once established a breeding site they rarely change islands, though most, except Abbott's, change their individual nest site. On Kure masked boobies nested in two groups separated by a belt of *Scaevola*, and although they were hardly 90 m apart only one bird, a female, switched groups (Kepler 1969). Nevertheless a male brown booby bred on Pearl and Hermes reef in 1967 and on Kure in 1969. Several individually recognizable adult red-foots were caught, though not breeding, on different islands in the north-central Pacific (Woodward 1972) and there is one recovery of a red-foot breeding on two different islands in the Hawaiian group. Mainly due to guano digging, individual Peruvian boobies may breed on more than one island.

Many cormorant species may change the location of their colony from time to time or (if that persists) their particular site.

The three non-endemic frigatebirds maintain permanent colonies, but as a consequence of their unusual breeding cycle individuals may not nest in the same part of the colony on successive attempts and perhaps sometimes swap islands.

In the Galapagos, marked birds appear to show that the red-billed tropicbirds of nearby Plaza and Daphne remain separate (Snow 1965). However, even if tropicbirds remain within a particular colony for life they do not keep within the same group or sub-colony and thus do not maintain a

specific site, though they may use it more than once.

Whilst there are benefits both from natal and breeding philopatry and from the exceptions, the actual stimuli involved in the choice of a breeding colony must often be complex. These may include the amount and nature of the breeding space available and the adequacy of the local food. The latter may relate to the total population of seabirds insofar as different species have overlapping food spectra. A simple version of this complex situation might be: if an individual can acquire a breeding site in a stable or growing colony (assessable behaviourally), perhaps usually and preferably its own, it does so. If it can then feed adequately enough to support breeding (assessable physiologically) it attempts to reproduce. Otherwise it remains a non-breeder until these conditions are fulfilled; perhaps many die before even attempting to breed.

Breeding cycle

General aspects

A seminal account of the relationship of seabird breeding and the marine environment is in Ashmole (1971). A breeding cycle commences not with egg-laying but with occupation of the breeding site. It ends when the bird disperses or migrates. A seabird tied to the colony loses feeding time, uses energy for travelling, increases the risk of injury when landing and departing (in some species a major cause of adult death), and faces possible predation on land. Within a species there is usually little option to reduce any component of the breeding cycle. For example, the Atlantic gannet lacks post-fledging feeding whereas Abbott's booby feeds its free-flying young for about six months. But gannets attend their sites for much longer than Abbott's booby before laying and after the young have left the colony. In both species these inflexible traits have evolved as essential adaptations to their feeding environment (Sp Acc). Nevertheless some pelecaniforms are fairly flexible, particularly in the pre-laying and post-fledging components. In no pelecaniform family except some endemic cormorants and possibly Ascension frigatebirds does

the entire breeding population remain at the colony throughout the year.

Rearing young might not be the most energy-expensive phase of breeding. Pre-laying attendance and incubation may be more demanding since the former often entails energetic display and site defence, and both phases may require long abstinence from feeding and debilitating attendance, perhaps at considerable cost in energy, for example, in maintaining body temperature. Each component of the breeding cycle faces its own selection pressures which differ between species and between populations. For example, 18 daylight hours on a gannet site in January may cost two full days' foraging time when climate, too, is energy demanding, prey may be difficult to locate, and feeding conditions inhospitable. In June 18 hours costs far less; days are long, temperature mild, mackerel inshore, and seas calm. The same scale of differences would not apply to the equivalent phases in the cycle of the red-footed booby. At the population level, the gannets of east and west Britain differ significantly in climate and food and on the east and west sides of the North Atlantic even more so. Again, in the Galapagos, pre-laying attendance in the flightless cormorant, which feeds within 100 m of its site, costs less than in the great frigatebird, whose feeding foray might require several days.

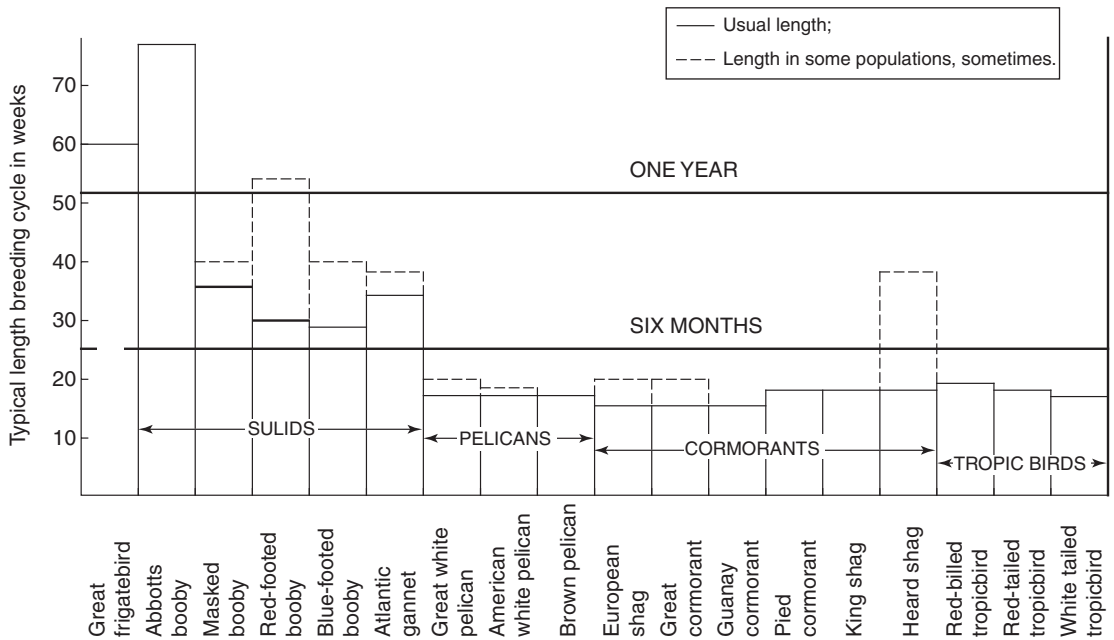
Trivers (1972) suggests that in most monogamous species breeding costs females more than males but field observations do not invariably support this. There are no peleciform studies specifically on this point but information on the length of incubation stints and the frequency with which chicks are fed indicate that in some species males, and in others females, take the larger share (Sp Acc). The position is complex because it may be that males and females have different daily energy requirements (see Wingham 1985) and therefore unequal stints may nevertheless cost the same. For example, male wandering albatrosses incubate more than females and lose weight at a greater absolute but lesser proportional rate. Thus both sexes lose approximately equal proportions of body weight during incubation (Weimerskirch 1992). All males and most females gain weight whilst at sea between shifts but males do so faster than females. The implications of such energetics for breeding costs may be considerable.

The hormonal changes which underlie the various stages of reproduction have been analysed for masked and red-footed boobies and red-tailed tropicbirds (Lormee *et al.* 2000). These authors measured plasma levels of luteinizing hormone, prolactin, testosterone and progesterone throughout breeding, and attempted to relate differences to aspects of the breeding cycle, such as the simpler display of tropicbirds and the duration of parental care. Particularly in boobies, testosterone levels were very low throughout breeding, which the authors relate to their year-round attendance at the colony. Prolactin increased during the pre-laying period but declined after the close-brooding one. In tropicbirds it remained about the same throughout, which they suggest facilitated parental care despite prolonged foraging absences. In all species, but especially boobies, females had higher prolactin levels which the authors associated with sex differences in parental care. These conclusions are debatable but fascinating.

Breeding strategies determine lifetime productivity and thus face strong selection pressure. Within the peleciform strategies have to cope with wide adaptive radiation, which encompasses a-seasonal, tropical regimes through to those of the Arctic and Antarctic. Strategies involve: (a) timing and frequency of breeding; (b) size of egg, clutch, and brood; (c) energy invested in the various components of breeding, some of which, like pre-laying attendance, can be truncated, or like post-fledging feeding, even omitted; (d) tendency to abandon eggs or young if conditions become unfavourable; (e) energy spent on attachment to breeding site and partner; and (f) size, spatial, and social characteristics of the breeding group. And strategies mesh closely with the species' wider web of adaptations embracing morphology, behaviour, and physiology.

Timing and frequency of breeding

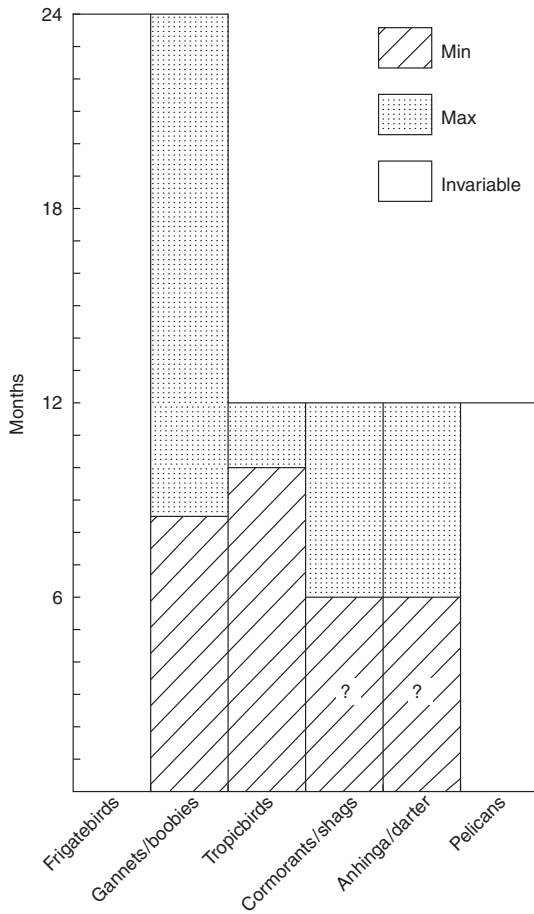
(Figures 3.4, and 3.5.) Birds lay at those times of year which overall produce most survivors to breeding age (Lack 1968). Peleciform breeding cycles range from almost continuous readiness to be triggered, through strictly annual, seasonal cycles, to loosely seasonal annual or biennial cycles. Some (frigatebirds and Abbott's booby) breed even less



3.4 The typical length of the breeding cycle in some pelecaniforms.

3.5 The frequency of successive successful breeding cycles (excluding 'rest' years).

<i>Family</i>	<i>Max. breeding frequency</i>	<i>Min. breeding frequency</i>	<i>Comment</i>
Pelicans	Once in twelve months	Once in twelve months	No pelican known to diverge from annual cycle
Gannets/ boobies	Once in 9–10 months (Blue-foot Brown)	Once in 24–36 months (Abbotts)	Annual breeding typical. Some intra-specific variability
Cormorants/ shags	12-months	12-months	Galapagos cormorant exceptional. Males breed once 13.3 months Females once 9.3 months
Anhinga/ darter	12-months	12-months	Double brooding possible
Frigatebirds	36–48 months	48-months	None except male magnificent frigate breeds less often than once in 48 months if successive cycles follow unbrokenly
Tropicbirds	9.5 months (White-tailed) 9–12 months (Red-billed)	12+ months	Non-breeding years probable



3.6 Intervals between successive successful egg layings in pelecaniforms, excluding possible 'rest-years'.

Note: The male magnificent frigatebird and flightless cormorant are partial exceptions; they abandon one cycle partway through chick rearing and may begin a second one with a new partner.

frequently than once in two years. Timing is usually determined by food, to fuel egg production, feed young or maintain adults in optimal condition during the most demanding phases of reproduction, which are not always those in which young are fed. Pre-laying and incubation demands prolonged attendance which may be practicable only at certain times of year when food permits. An important factor in a seabird's relationship with food is the predictability with which it can locate it; the actual capture is much less demanding than finding it.

In strongly seasonal latitudes, breeding seasons may be sharply defined and in a given locality a species' mean laying date may be highly consistent from year to year. The Atlantic gannet has a clearly defined annual cycle, the limits of which are set at one end by selection against too-late fledglings and at the other by inclement weather and constraints on food and foraging time. But tropical seabirds may breed more opportunistically. Over their lifetime, many individuals of most tropical pelecaniforms are likely to lay in most or all months of the year. Where non-seasonal breeding is favoured, the advantage gained in lifetime breeding frequency must outweigh any decrease in breeding productivity which could result from laying (as it turns out) at a sub-optimal time. But where there are inadequate environmental cues to enable a bird to predict the less-favourable periods it would be disadvantageous to restrict laying to any one time of year. In such circumstances, as in the Galapagos, food might become scarce during the growth of the chick even though, previously, it had been adequate. Here, the best strategem is to use food as a proximate trigger to initiate breeding, thus ensuring that, at least, courtship, nest-building, and egg production are adequately fuelled. The red-footed booby on Tower (Galapagos) is such a case (Nelson 1968). As for the remainder of the cycle, chance will in any event play a large part in the outcome.

Many pelecaniforms, including some sulids, tropicbirds and frigatebirds, are loosely or very loosely seasonal breeders, variably intermediate between highly predictable seasonal laying and year-round laying. This may accommodate environmental factors which though somewhat predictable are nevertheless variable. But the detailed long-term information needed to clarify these complex patterns is not available.

Pelicans

Within the family there are continuous, non-seasonal and opportunistic breeders and annual, highly seasonal ones. The American white pelican may arrive in flocks on its Wyoming nesting grounds during late April or in May, when most of the lakes are still frozen (Schaller 1964), and quickly engage in conspicuous flight-circling. Breeding

colonies can form rapidly. It may then lay in late May or June. Further south this schedule is three or four weeks earlier. But even in this species the spread of laying may be so considerable that discrete groups on the same island, as on Gunnison Island, may coexist at very different stages, some with naked young whilst others are ready to fly (Behle 1958). A complete breeding cycle may take only 14 weeks. Colonies are deserted by about mid-September and the birds migrate southwards.

The great white pelican breeds seasonally in Russia and eastern Europe and even in parts of Africa, but continuously or opportunistically in other parts. In Africa large colonies may be more or less continuously occupied but by different groups of birds, 'when one group vacates an area others immediately occupy it' (Brown and Urban 1969). At Lake Shala the breeding population of 2,500–5,000 pairs was made up of groups of 300–1,200 pairs, each group internally synchronized but out of phase with the others. Each occupied part of the breeding area for about three months after which the young, in pods, moved out of the nesting area, thus freeing a patch of breeding ground. This unusual adaptation enables the great white in this area to exploit flushes of food in a way that would not be possible were the whole population to breed synchronously. Similarly, the Australian pelican exploits temporary flushes (Marchant and Higgins 1990). In neither species is there evidence that any pair breeds more than once a year.

The brown pelican varies its breeding regime with area. Most North American colonies lay mainly March–April (Johnsgard 1993), though the most southerly may be occupied almost continuously. Moreover, in any given year the timing of laying differs in adjoining colonies and the same colony varies in different years. The Peruvian race of the brown pelican, like most Peruvian guano birds, may breed throughout the year (Murphy 1936).

Since at least four of the seven pelican species (probably five since the spot-billed is unlikely to be seasonal everywhere even though it is so in parts of India) may lay in most months, and the others have, in some localities, a wide spread of laying, it is inaccurate to define the family as essentially seasonal breeders. Rather, they are highly adaptable,

as they are, also, in their wide range of climatic and feeding regimes.

Gannets/boobies

The only strictly annual and seasonal breeder with a highly predictable mean laying date is the Atlantic gannet. Defining 'seasonal' as peak (mean or median) laying at the same time each year, which is a better criterion than the date of the first egg, British gannetries vary by between one and three weeks in mean laying date but the same gannetry, in different years, by only a few days. Australasian and African gannets are much less consistent, the same colony varying by several weeks in different years. Their spread of laying, also, is much greater than the Atlantic's; possibly their food resources are more variable.

Among boobies the annual cycle is more modifiable. Although *all* boobies except Abbott's may breed annually, only the masked has an approximate annual cycle throughout its range, and even in this species the spread of laying in any one population can be very considerable (Nelson 1978b). In all the other boobies at least some populations, or populations at some time, breed more frequently than once every 12 months (the usual case) or less frequently.

All booby species are loosely seasonal; any given population shows a higher incidence of laying in some months than in others but globally all of them except Abbott's lay in any month. Regardless of particular month, brown, blue-footed, and Peruvian boobies typically lay at intervals of between eight and ten months. Abbott's booby lays only once in two years or sometimes twice in three (Nelson and Powell 1986). Some populations of the red-footed booby may lay less frequently than once a year but, excluding replacement layings, more than once in two years.

In most populations of brown and blue-footed boobies increased frequency of breeding seems to be related to an a-seasonal environment and (in some areas) unpredictable food. The nine-monthly cycle of the brown booby on Ascension is not a fixed interval comparable to the annual cycle of temperate seabirds. Rather, brown boobies *can* breed at that interval, remaining at the colony and therefore able to respond to favourable conditions (Simmons 1970).

Often, the previous attempt will have failed and the pair may quickly begin another clutch. Alternatively, failure may be followed by a variable period before the next breeding cycle begins. Underlying this variability may be a loosely cycling periodicity as a consequence of some months being on average most likely to see the initiation of clutches. Likewise, the Galapagos area experiences seasonally unpredictable food shortages and its blue-footed boobies may lay in any month. As in the brown boobies of Ascension, blue-footed booby cycles are unusually short in comparison with other sulids; successive, successful layings may occur eight months apart. Elsewhere, both these boobies may be annual breeders.

Although closely related to the blue-footed, the Peruvian booby lives under conditions very different from the Galapagos. In most years food is superabundant and egg-laying is markedly seasonal and annual. But after ENSO and the ensuing population crashes, laying becomes less seasonal and more frequent.

In Galapagos red-footed boobies, and especially in Abbott's booby, comparatively infrequent laying is a consequence of the long breeding cycle due mainly to protracted dependence of the young, associated with climate and related feeding (Sp Acc). Thus, like pelicans, sulids are flexible in their breeding regimes and the fixed, seasonal, annual cycle is by no means the norm. Rather, each species and population has adapted to local circumstances.

Cormorants/shags

These breed from well within the Arctic circle to 65°S, a range unequalled by any other pelecaniform family and exceeded only by the gulls/terns/skuas. With this distribution goes extremely flexible breeding regimes. Most cormorants lay over a protracted period in most parts of their range, or they lay in all months. But a number of cool-temperate species—for example, in the north, the great cormorant, European shag, pelagic, double-crested, red-faced and Brandt's cormorant; and in the sub-Antarctic, the blue-eyed shags,—show fairly compressed and annually consistent laying periods. But even in these, pre-laying attendance and mean laying date is highly variable.

The British and north European populations of the great cormorant and European shag are probably

as annually consistent and restricted in their main laying period as any cormorant. Even so, their mean laying date varies by six weeks or more in the same locality in different years (personal observation); five or six times as much as in the Atlantic gannet.

As inshore feeders, with restricted foraging ranges, cormorants face selection pressures different from those confronting pelagic feeders such as most boobies, the tropicbirds, and the frigatebirds. They need to gather food quickly, dependably and in sufficient quantity to feed comparatively large and fast-growing broods. They cannot breed successfully where food is thinly distributed in widely separated patches and in an unpredictable pattern. And the adults, lacking fat deposits (an adaptation for achieving neutral buoyancy), must feed regularly and extensively (Ainley 1984). But under favourable conditions they can breed in great concentrations. Then feeding competition is likely to be more significant than among blue-water pelecaniforms and a wide spread of laying should be adaptive, as should the ability to vary the breeding season in relation to climatic and feeding conditions.

Cormorants breed annually or more frequently and none consistently less often than once a year. The flightless cormorant, an extreme example of a local, inshore feeder, may attempt to breed several times in a calendar year (Harris 1979a), and under favourable conditions the guanay and Cape cormorants may breed more or less continuously (Murphy 1936; Brown *et al.* 1982). The European shag very occasionally rears two broods in a year (Wanless and Harris 1997).

Anhinga/darter

Both species have extended breeding seasons; in the darter's case breeding may occur year-round. In this species Bowen *et al.* (1962) reported two separate periods of egg laying (Ghana) between June and November but, although sometimes cited as such, with no clear evidence of double-broodedness. In Australia, separate peaks were not due to double-broodedness (Vestjens 1975).

Frigatebirds

This is the only pelecaniform family in which no species can breed as often as once a year. Their

protracted breeding cycle (15–18 months or more) restricts successful breeding to, at most, once in two years. The single partial exception is the male magnificent frigatebird which may abandon one cycle partway through and begin another with a new female, thus breeding once each year (Diamond 1972; Barbuda, Caribbean).

Frigatebirds are pan-tropical, with a wide latitudinal range encompassing largely a-seasonal to markedly monsoonal (or other seasonal) climates. In some regions the great frigatebird is a seasonal egg-layer whilst elsewhere laying has a much wider spread. The lesser frigatebird, also, is a typically seasonal but also a protracted layer. On Aldabra, for example, females which eventually laid had previously settled over a total period of some 200 days (Reville 1980). Magnificent frigatebirds are seasonal but extended layers. Of the two endemics, the Ascension frigatebird may lay in any month (Stonehouse and Stonehouse 1963) whereas the Christmas frigatebird is markedly seasonal (Nelson 1976), a difference explicable by the seasonal, monsoonal environment of the latter.

Seasonal breeding in frigatebirds may relate to the communal nature of the male's display. Lacking seasonal changes, it would presumably be difficult for males to synchronize breeding condition and hence to display communally unless they had an endogenous timer in the form of a circannual rhythm. Communal display is extremely important in frigatebirds since clumped nesting groups stem from prior display nuclei. Clumping in turn affects the synchronization and thus the success of breeding. The protracted laying period of frigatebirds presumably results from birds getting out-of-phase with each other, a situation which is exacerbated by the high failure rate and the habit of taking 'rest' years between breeding attempts (Coello *et al.* 1977). Frigatebirds may, in fact, breed less frequently than any other seabird which, incidentally, makes human depredation of adults extremely serious.

Tropicbirds

These inhabit warm, highly saline, blue-water regions but, like frigatebirds, their range includes widely different climatic regimes. All three species can be found with fresh eggs in any month.

On Cousin Island, Aldabra, and Ascension, the white-tailed breeds all year round with apparently no consistent periodicity, although there are periodic but non-seasonal peaks coinciding with this species' approximate nine-month breeding cycle. But whilst Ascension has no marked seasons and its seabirds lay at any time of year, Aldabra has a 'dry' season (southeast trades, March–October) and a calmer 'wet' season (northwest monsoon). Moreover, the red-tailed tropicbird on Aldabra showed two pronounced peaks of breeding and two troughs, the latter coinciding with the dry season (Diamond 1975b). There is considerable overlap in the diet of these two species and it is not clear why they have different breeding regimes on the same island.

The red-tailed and red-billed tropicbirds tend to lay annually or slightly less than once a year. For example, the red-billed breeds at approximately 11-month intervals on Ascension (Stonehouse 1962) and 12-monthly on Plaza, Galapagos (Snow 1965). But on Daphne, closely adjacent to Plaza, individuals appear to breed as often as possible, which may be at less than 12-monthly intervals, perhaps because nearly 70 per cent of breeding attempts fail due to intense competition for breeding sites. It has not been shown that the same pair will ever breed successfully more than twice in two years. Woodward (1972) suggested that on Kure the red-tailed, if successful, will not breed the next year.

Figure 3.7 shows the differences in composition of pelecaniform breeding cycles.

Pre-laying attendance

Between returning to the colony and egg-laying, birds consolidate site-ownership, acquire a stable partner and build a nest.

Pelicans compress pre-laying attendance. Ground-nesters select a nest-site only after the pair-bond has been initiated. Pre-laying tenure is short, even in seasonal breeders, and energy reserves are not depleted by lengthy defence of site. Moreover the eggs cost little to produce. Both factors help pelicans to invest much energy in chick-rearing, during which a huge biomass is quickly produced.

Sulids have several options. The pan-tropical boobies can maintain regular contact with the

3.7 The composition of breeding cycles in pelecaniforms.

Family	Pre-laying attendance		Incubation period		Period before young fly		Period parents feed flying young		Adult site-attendance after young disperse		Total length successful breeding cycle		Comment
	L	S	L	S	L	S	L	S	L	S	L	S	
Pelicans	2–4 weeks	3–4 days	35 days all species c. 31–32 days	30 days	12 weeks	10–11 weeks	Possibly 3 weeks (Spot-billed)	None (most pelicans)	Adults disperse soon after young fly		Little difference typically c. 19 weeks		Pre-laying attendance excludes earliest arrivals which do not attend sites or begin breeding activity.
Gannets/ boobies	c. 14 weeks (Atlantic gannet)	c. 3 wks (several boobies)	55 days (Abbott's booby)	c. 42 days (others)	c. 24 wks. (Abbott's)	12 wks. (Atlantic gannet)	c. 24 wks (Abbotts)	None (gannets)	c. 10 wks. (Atlantic gannet)	Boobies may disperse after few days	c. 60 wks. (Abbotts)	c. 26 wks (several boobies)	Major variables: (1) Pre-laying attendance. (2) Post-fledging feeding
Cor-morants/ shags	Several months (inter-mittently (Macquarie shag))	3–4 days (some Great cormorants)	32 days (com-monly)	22 days (3rd. egg, Cape cormorant).	11–12 wks. (some Antarctic) shags	c. 6 wks. (Double crested)	36 + wks. (Galapagos cormorant)	2–3 wks (Double crested)	A few species attend sporadically most of year	Most cor-morants disperse almost immedi-ately	Typically 140–50 days	96–100 days (Double crested)	Many cormorants leave nest before able to fly.
Anhinga/ darter	?	Less than 7 days	c. 28 days		8–8.5 weeks		Short or None		Not known to occur		Less than 15 weeks		Lacks well defined seasonal breeding and is commonly resident, figures for pre-and-post breeding attendance imprecise.
Frigatebirds	Probably 4–6 weeks (Great frigate)	Probably few days (Lesser frigate)	53–55 days (most species)	c. 41 days (Lesser frigate)	24 + wks (probably all species)		24–32+ weeks (Great frigate and probably others)	c. 24 weeks	None	None	568+ weeks	60 weeks	Fairly accurate fledging periods known only for Great and Lesser frigate (Aldabra). Post-fledging feeding very variable but longer periods than given here probably not representative.
Tropicbirds	c. 12 wks (Red-tailed) (Intermittent)	c. 2 wks. (White-tailed)	c. 43 (Red-tailed)	41–42 days (White-tailed)	85–90 days (Red-tailed Red-billed)	75–80 days (White-tailed)	Probably none		Little or none		c. 33 wks.	c. 19 wks.	Fledging period highly variable; figs. given here are approx. averages.

L = Longest
S = Shortest.

breeding island, or disperse locally within the island group, or become nomadic, perhaps remaining at sea for long periods outside the breeding season. Although Dorward (1962) reported that on Ascension brown boobies were usually absent from territories outside the breeding 'season', Simmons (1967b) found that some of the birds on two of the Georgetown stacks maintained daily contact throughout the year. On Christmas Island (IO) local groups may disappear during the non-breeding season but some birds can be seen year-round. Similarly, colonies of the red-footed booby retain part of their adult population year-round. However, there is extensive dispersal of post-breeding adults which may roost on the island either away from their sites or in the (inactive) breeding area. On Aldabra during July and August when few birds were breeding, the nesting trees still held about half the number present at the height of the season and there were roosts elsewhere on the island (Diamond 1978). On Ascension, masked boobies occupied the breeding area for the entire year (Dorward 1962), though not at full strength, whilst on Kure there was a clear separation between breeding and non-breeding seasons. Blue-footed and Peruvian boobies may be seen at their breeding colonies throughout the year but in fluctuating numbers. In the Gulf of California, blue-footed boobies disperse when not breeding and turn up in groups, with brown boobies, on rocks and islands where they do not breed (Anderson *et al.* 1978). On Christmas Island, experienced Abbott's boobies currently without breeding duties leave entirely during the monsoon period, returning in April, some weeks before they lay again.

These marked differences presumably reflect feeding economies. Probably, too, more time is spent at the colony if there are few (or no) alternative land-falls. But no more than three or four weeks of pre-laying attendance are actually required.

In strong contrast, attendance in Atlantic gannets is clear-cut. They vacate the colony completely for a period of winter nomadism and resume full territorial behaviour at least two months before laying. Although energetically costly, pre-laying attendance reduces the probability of site-usurpation. In the tightly structured gannetry an empty site is conspicuous and desirable, competition fierce, and site

fidelity strong. This applies much less in the loosely structured booby colony. Experienced breeders are much less faithful to their sites than gannets, and even the heart of the colony may contain non-breeders, pre-breeders, and immature birds. More like boobies, the African gannet may frequent its colonies throughout the year, though mainly from August to late May. Although most adults disperse soon after the chicks have fledged, on Bird Island (Lambert's Bay) a few hundred, mainly males, may roost at night. Out-of-season attendance ranges from a few to almost the full complement (Crawford *et al.* 1983). The Australasian gannet does not occupy its colony in strength outside the breeding season but it varies much more than the Atlantic in its return date, departure and duration of pre-laying attendance. In these, as in other respects, the Australasian and African gannets, more than the Atlantic, resemble the boobies.

Cormorants range from continuous, if sporadic, colony attendance to seasonal occupancy. The commonest pattern in species which disperse after breeding is for a variable date of return, experienced males first, followed by variably timed laying depending on local circumstances. Even cormorant species which remain near to their colonies vary in their attendance patterns from year to year and in the duration of the pre-laying period. The Antarctic shag may assume nuptial plumage by mid-May but return to the colony only in mid-July, delaying courtship until mid-September. The first eggs may be laid as long as three months after return. The South Georgian shag may return to the colony by mid-July but lay in mid-November or early December. The Crozet shag never entirely deserts its colony and occupies its nest-site permanently for the three weeks before the (variable) laying date. The European shag may return more than two months before the first egg is laid. At the other extreme the great cormorant in the Arctic may arrive at its Greenland colonies in early April and the first eggs may be laid within a month, whilst in Holland they may be working on their nests of the previous year a mere two days after arrival. Yet in Scotland, six weeks may elapse between males stationing themselves on potential nest-sites and the start of building. On the Farallons, Brandt's cormorant at first roosts at its site from late

afternoon to early morning but leaves it for much of the day; whilst on the same island the pelagic cormorant may be seen on its site as a pair even during winter and early spring. In this cliff-nester suitable sites may be limited and continuous occupancy an advantage. This phase in cormorants is evidently flexible but site-establishment, pair-bonding and nest-building take three weeks or more.

In the anHINGIDS the pre-laying period is short. Neither species disperses far from the breeding area; some anHINGIDS arrive at the breeding locality already paired.

Frigatebirds lack a definitive site prior to pair-formation. A displaying male may move from place to place until he has paired, at which point the twig or branch on which he displayed becomes the nest-site. A male may thus spend considerable energy for at least a month at the colony before acquiring a mate. Reville (1980) noted that between two and three weeks before display became widespread, some male great frigatebirds, mostly with small gular sacs, gathered in clusters of 8–10 birds adjacent to nesting areas. The long 'rest periods' between successive breedings may result from the stress of the lengthy breeding cycle.

At most tropicbird colonies, the interpretation of site attendance is complicated by the continuous presence of breeders. Also, two pairs may attempt, simultaneously, to attend the same site. On Cousin Island (Seychelles), white-tailed tropicbirds occupied nest sites, usually singly, for a month or two before laying (Phillips 1987). In several cases, mating was recorded the first time that the pair were seen together—perhaps established pairs re-uniting. Fidelity to site and mate, common in tropicbirds, would facilitate this. Similarly in red-tailed tropicbirds, reoccupation by a specific pair, episodic at first but increasing over several weeks, fits more easily with pelagic foraging than would near continuous occupation for a prolonged period, but is an option only where there is a fixed site and pair-bond. It could not happen in frigatebirds.

After mating, tropicbirds may be absent for two to four weeks, making altogether one to two months between first return and egg-laying (white-tailed on Cousin). The same species on Ascension, however, took a minimum of 16 days during much of which the birds were absent, possibly accumulating reserves

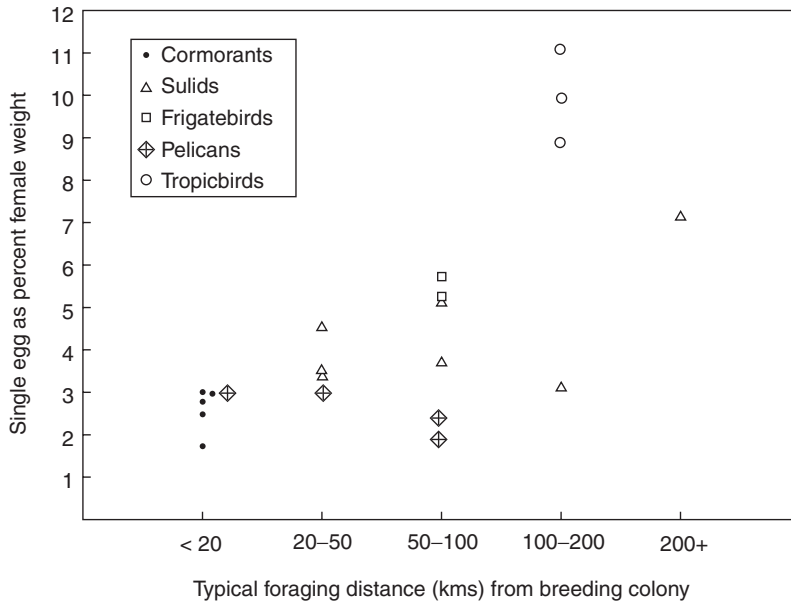
for egg-production and incubation. That this may be important is suggested by the fact that despite intense competition for nest-sites and frequent, damaging usurpations, Ascension birds often left the site unguarded even within hours of laying (Stonehouse 1962).

The egg

Because eggs cost energy, their production relates to the species' food resources and foraging pattern and to the developmental pattern of the embryo and hatchling (see Montevecchi and Porter 1980 for key review). Seabird eggs vary in size, composition (size and density of yolk and amount of albumen), the nature of the egg shell, shape, colour, time taken to form, relationship between egg-size and the female's age and experience, and between egg-size and success in producing a hatchling and eventually a fledgling.

Egg size

(Figures 3.8, 3.9 and 3.10) In uniparous peleciforms (frigatebirds, tropicbirds, five sulids but no pelican, cormorant or anHINGID), the single egg never constitutes more than about 13 per cent of female weight (white-tailed tropicbird), and in most cases less than 4 per cent compared with 2.3–4.7 per cent in penguins, up to 25 per cent in tubenoses, and 40 per cent in the blue-gray noddy which lays the heaviest egg of any bird (Rahn *et al.* 1984). In part, the smallness of the peleciform egg reflects the fact that egg-mass relative to that of the female is less in large than in small birds and therefore peleciform eggs are not proportionately larger than those of smaller seabirds. In fact, however, cormorants and pelicans lay very small eggs (as little as 2 per cent of female weight Figure 3.9) compared to other large seabirds, although in multiparous species the entire clutch may represent a more significant energy cost. Moreover, at least in cormorants and sulids, even in such small eggs the yolk as a percentage of egg content is low compared with other seabirds. It averages only 17.5 per cent in pelicans, 19 per cent in sulids and 21 per cent in cormorants (Rahn *et al.* 1984; Bugden and Evans 1997) compared with 38 per cent in procellariiforms. Peleciform eggs are thus comparatively cheap to produce. Rahn *et al.*

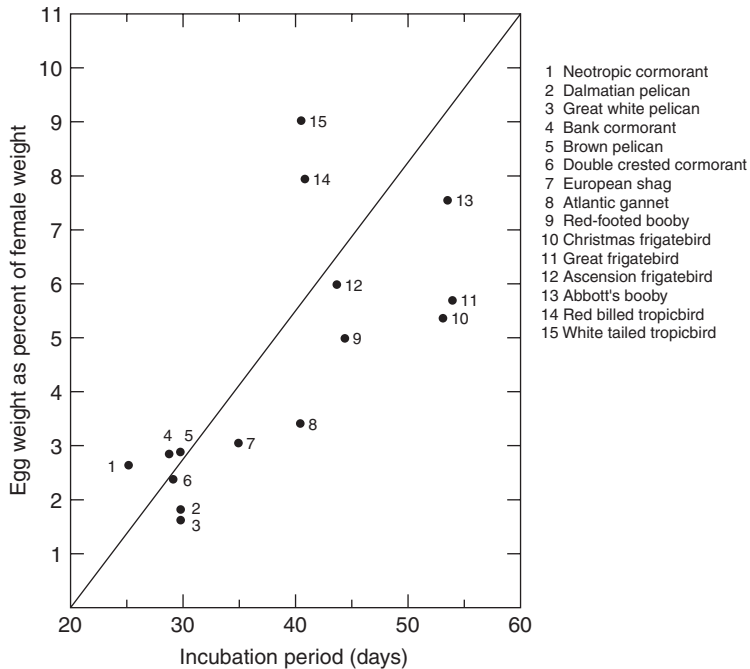


3.8 Egg mass in relation to foraging range.

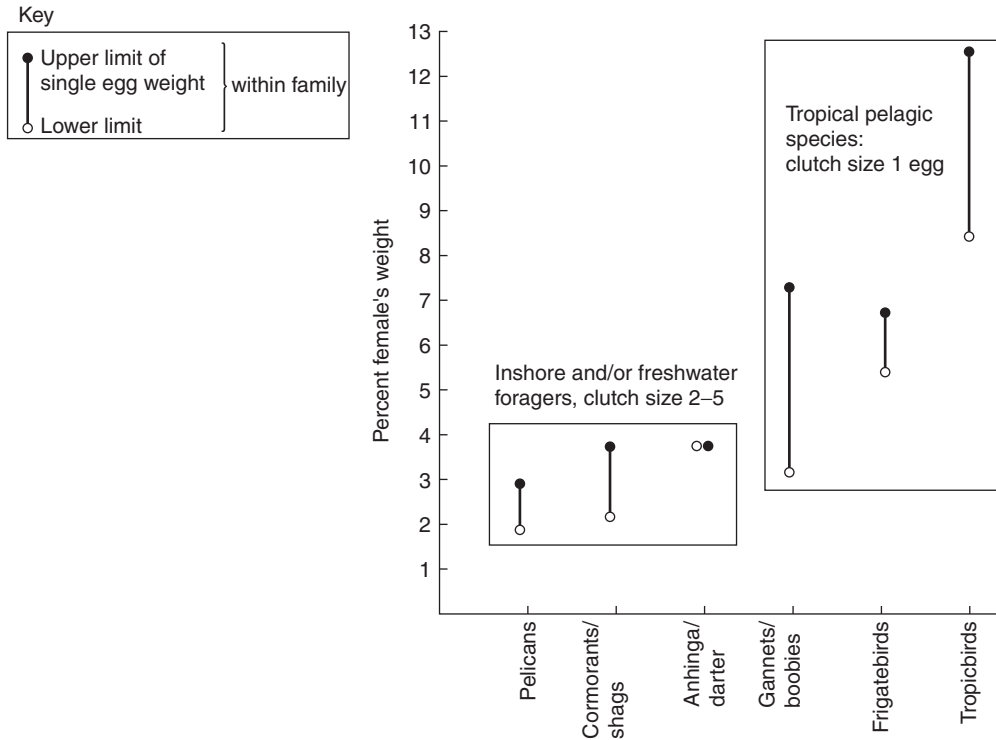
Notes: 1. Great variation in weight of adult female, especially in pelicans.

2. Typical foraging distance an approximation only.

3. Tropicbird chicks are downy and active; all other pelecaniforms are nidicolous.



3.9 Egg as percent of female weight in relation to length of incubation period.



3.10 Range of egg size within pelicaniform families in relation to female weight, clutch size and foraging mode.

calculate that it costs five times as much to produce a petrel's egg as that of a cormorant or of some booby species. This investment is part of a species' adaptedness to features such as how much foraging effort is required to fuel it, how likely it is that the egg will have to be abandoned and to what extent the hatchling's degree of development affects its chances of survival, which bears directly on the species' feeding/foraging regime. Two species may differ greatly in these and other respects even though both may lay a single-egg clutch.

The pelicaniform egg is small partly because in all except tropicbirds the hatchling is altricial. Eggs which produce precocial hatchlings have bigger yolks which enable the young to achieve advanced development before hatching. Tropicbird hatchlings are downy, but because they are unable to leave the nest and have to depend on their parents for food they are defined as semi-altricial. Their eggs have more yolk and a greater energy-content than those

of altricial species such as sulids. The red-tailed tropicbird's egg contains 24.4 per cent yolk and 1.635 Kcals/g-1 wet weight, whilst that of the red-footed booby contains only 15.8 per cent yolk and 1.009 Kcals/g-1 wet weight (Pettit *et al.* 1984). And this comparison directly compares two uniparous, pelagic, blue-water species. But also, yolks form a food store for the hatchling. In the Adelie penguin, for example, about half the yolk is still available after hatching (Ainley 1975). This figure is only 16 per cent in the double-crested cormorant (Johnsgard 1993). Both egg-size and the energy density of the yolk contribute significantly to the survival of the unfed hatchling (Montevecchi and Porter 1980). Newborn tropical pelagic pelicaniforms are more likely to face starvation than are temperate, inshore feeders. One would therefore expect eggs of the former group to be larger, and in fact frigatebird eggs *do* have more yolk and a greater energy content than those of cormorants or

pelicans. Within the Sulidae, Abbott's booby has a particularly large egg (8.5 per cent of female weight) and the Atlantic gannet a particularly small one. The former is far more likely to face post-hatching starvation and develops extremely slowly (Sp Acc), which correlates with large egg size. Even within a species, regional differences in egg-size relate to the availability of food. Red-footed boobies on the Indian Ocean Christmas Island lay proportionately smaller eggs than their counterparts on Tower Island, Galapagos, which are notably subject to food shortage (Nelson 1968). Comparably, the common tern laid larger eggs and clutches in an area with better quality of food (Nisbet 1978). Nestlings of the European shag from larger eggs grew faster and were heavier at fledging and tended to survive better than those from smaller eggs (Amundsen and Stokland 1990). However, parental quality may be involved here since larger eggs come from heavier females. This, though, cannot apply to differences within a clutch, where larger eggs are still at an advantage.

Whilst food is clearly a determinant of egg-size, there is also a genetic component. Some females lay bigger eggs than others from the same colony, and egg-size tends to remain a constant individual trait from year to year, indicating that the foraging quality of the individual is unlikely to be the sole cause. In the European shag, even when comparing females of the same age, egg volume decreases as the season progresses (Sp Acc). However, later-laying females tend to be smaller birds. The same is true of kittiwakes (Coulson 1966), but whereas in that species egg-size declines only slightly as the season advances (though clutch-size declines rapidly) it is the other way round in the shag.

Egg-size and breeding success

Within a species, chicks from bigger eggs tend to grow faster and are more likely to fledge than those from small eggs (Furness 1983 provides a good critique and references), but the precise relationship is complex. For example, in 1970 the survival of herring gull chicks was closely related to hatching weight (Parsons 1970), but Davis (1975) found no such correlation. This contrary result may be an effect of the age structure of the population. In many

species egg-size increases with age of female, up to a certain age, but then decreases. Thus smaller eggs, but from very experienced females, may be more successful than larger ones from inexperienced females. This example suggests that the effect of egg-size on chick growth and survival may be readily surpassed by food and the foraging ability of parents. In Norway the growth of kittiwake chicks was not related to egg weight, but in England, Thomas (1983) found that in two-egg clutches a 10 per cent increase in egg volume appeared to result in an 8 per cent increase in hatching success and a 4 per cent increase in fledging success. However, in the Manx shearwater (Brooke 1978a, 1978b), fulmar (Ollason and Dunnet 1978) and some other species, there appeared to be no such relationship. These findings suggest the overriding influence of local food.

One might expect hatchling-size to be a constant proportion of egg-size but Furness showed that in the great skua hatching weight was a higher proportion of small than of large eggs. Since larger eggs contain proportionately more water and albumen they may lose more weight during incubation.

Egg composition (Figure 3.11)

Birds' eggs differ in yolk content, water and fat content of yolk, and in the protein content of the albumen. As an essentially altricial Order, peleciforms fall within the range of other such groups in the percentage of fat and protein in the yolk, at about 57–63 per cent dry weight (Williams *et al.* 1982). Values are a little higher in anseriforms and galliforms but much the same in tubenoses and penguins. Some peleciforms have yolks with a low fat content, for example 25 per cent in gannets and pelicans compared with 37 per cent in geese. Ricklefs and Montevecchi (1979) note that the Atlantic gannet has a lower percentage of yolk and of fat within the yolk than any other seabird.

The relationship between yolk content and precocity is complex and ambiguous. Although fully precocial species do have the highest proportion of yolk, other hatchling types do not follow a simple pattern. Altricial pigeons have more yolk than sub-precocial grebes, and the semi-altricial tubenoses have more yolk than many sub-precocial taxa (Williams *et al.* 1982). The length of time a hatchling

60 Pelicans, Cormorants and their relatives

3.11 Egg composition and hatchling precocity; the weight (g) and constituents of the eggs of 11 pelecaniforms. (From Williams *et al.* 1982.)

Family and species	Eggs sampled n	Whole egg weight		Percentage of whole egg formed by			Percentage of egg contents formed by	
		Mean	Range	Shell	Yolk	Albumen	Yolk	Albumen
Tropicbirds								
<i>Phaethon rubricauda</i> ^{2,3}	1	72.5		10.3	24.8	64.8	27.7	72.3
<i>P. aethereus</i> ^{3,4}	1	56.0		9.8	32.1	58.0	35.6	64.4
Cormorants/shags								
<i>Phalacrocorax atriceps</i> ⁵	7	50.5	(44–55)	13.2	20.7	66.1	23.9	76.1
<i>P. capensis</i> ^{3,6}	—	38.0		16.1	12.8	71.1	15.4	84.6
<i>P. capensis</i> ⁷	8	34.9	(32–7)	13.5	21.2	65.3	24.5	75.5
<i>P. carbo</i> ⁸	—	42.0		—	—	—	17.1	82.9
<i>P. carbo</i> ⁷	5	52.4	(37–60)	16.4	18.1	65.5	21.7	78.3
<i>P. coronatus</i> ⁷	5	22.6		14.2	24.3	61.5	28.4	71.6
<i>P. melanoleucos</i> ⁹	1	26.0		8.1	15.8	76.2	17.2	82.8
<i>P. neglectus</i> ⁷	4	46.7	(44–51)	13.2	17.5	69.2	20.2	79.8
<i>Stictocarbo punctatus</i> ⁹	3	40.4		9.2	15.8	75.0	17.4	82.6
Gannets/ boobies								
<i>Morus (b) bassanus</i> ¹⁰	10	117.7		12.1	15.5	72.5	17.6	82.4
<i>Morus (b) capensis</i> ⁷	5	97.8	(80–113)	15.5	17.9	66.6	21.2	78.8
<i>Sula leucogaster</i> ^{3,11}	—	—		12.5	16.0	71.5	18.3	81.7
<i>S. nebowxii</i> ^{3,11}	6	52.8		9.9	—	—	—	—
Pelicans								
<i>Pelecanus occidentalis</i> ^{12,13}	6	92.1	(77–102)	12.2	26.0	66.4	28.1	71.9
<i>P. onocrotalus</i> ⁷	1	203.8		14.6	12.2	73.3	14.2	85.8
<i>P. onocrotalus</i> ^{3,14}	54	181.6		—	17.1	—	—	—

Notes: ¹All pelecaniform birds have altricial hatchlings except tropicbirds whose hatchlings are semi-altricial.

²Diamond (1975b).

³Age and freshness of eggs not stated.

⁴Harris (1969).

⁵Williams & Burger (1979).

⁶Berry (1976).

⁷Williams *et al.* (1980).

⁸Heinroth (1922).

⁹Grau (1984).

¹⁰Ricklefs & Montevicchi (1979).

¹¹Nelson (1978b).

¹²Lawrence & Schreiber (1974).

¹³Some eggs contained well developed embryos.

¹⁴Jones (1979).

has to survive before the first feed varies, within the Sulidae for example, from less than an hour in the Atlantic gannet to (potentially) several days in some populations of tropical boobies. This must influence the evolution of yolk content and the correlation between egg composition and hatchling precocity.

Some seabirds lay down yolk more quickly than others. Among peleciforms, the spotted shag and pelagic cormorant took 12 days, about half the time required by the grey-faced petrel (Grau and Astheimer 1982).

Sibley and Ahlquist (1972) conclude, in their review (Chapter 1), that the patterns of egg-white proteins in peleciforms are uniform in the various cormorants (16 species examined) and show a marked similarity to sulids (6 species examined). Sulid patterns are themselves quite uniform and somewhat resemble pelicans (2 species studied). Tropicbirds resemble frigatebirds (3 species examined) but differ from core peleciforms, a separation which agrees with other criteria.

Eggshell

With increasing egg weight, shell weight increases disproportionately rapidly—approximately as the square root of egg weight (Ar *et al.* 1979). Thus shells are proportionately heavier in heavy than in light eggs and also in precocial than altricial species. However, according to Williams *et al.* (1982), out of four seabird Orders only the peleciforms showed the first of these relationships and that barely. The thinnest peleciform shell is thicker than the thinnest penguin's, albatross's or gull's, but the thickest peleciform is not quite as thick as the thickest in these other groups. Even within the peleciforms, species with light eggs may have proportionately heavy shells, for example 14.2 per cent of 58 g in the great cormorant but only 11.6 per cent of 105 g in the Atlantic gannet, despite the latter's underfoot incubation, which puts considerable pressure on the shell. Shells of cormorant eggs consistently form a higher proportion of whole-egg weight than in other altricial groups and even than in some semi-precocial ones. Along with penguins and guillemots, cormorants produce the heaviest shells.

Eggs must withstand the pressure of the incubating adult, abrasion against other eggs and accidental

knocks. Shell thickness, therefore, may be adapted to the nature of the substrate and the method of incubation. Those albatrosses which build nests have lighter eggshells than fulmarine petrels which nest on open ground or on rock, where impact resistance is useful (Warham 1990). The Atlantic gannet, which builds substantial, well-lined nests, has proportionately lighter shells than the African, which lays its egg on bare ground or guano. Frigatebirds and tropicbirds, which are light and do not incubate underfoot, have smoother, thin-shelled eggs. Penguins, which usually breed on ice, rocks or hard ground, have heavy shells. Williams *et al.* (1982) note that cormorants, penguins, and auks, all heavy shelled, are pursuit-swimmers with legs placed well back. They are thus clumsier on land and more liable to knock their eggs, many of which are accidentally lost. By contrast, grebes and divers, though even clumsier, make nests of soft vegetation, have lighter eggshells and lose fewer eggs through accident. A tangential but perhaps important point is that the requirement for calcium for the shell, greatest in heavy ones, may necessitate comparatively long laying intervals during which the minerals are mobilized and deposited. Long hatching intervals are impracticable in multiparous species in which the young leave the nest soon after hatching. However, calcium should be readily available to fish-eaters.

The shells of sulids, pelicans and cormorants, but not of frigatebirds or tropicbirds, are covered with a chalky layer of vaterite (calcium carbonate) which quickly becomes scratched and discoloured. It may be protective and in gannets helps the webs to gain purchase on the egg's surface. Apparently there are no peculiarities of shell structure in peleciforms. The pores on the surface lead into channels which run straight to the eggshell membrane, through which gaseous interchange occurs. In peleciforms, as in grebes, divers and tubenoses, the pores are simple, round in cross-section and with a slightly funnelled opening. Tyler (1969) could not distinguish between pelicans, sulids, cormorants and frigatebirds in any of the structural characters which he studied, although pelicans had more shell nitrogen than the others.

During incubation birds' eggs lose 14–15 per cent of their initial weight (Rahn *et al.* 1976), the

amount varying with the temperature of the egg which depends on the environment and on the incubation idiosyncrasies of the species, such as leaving the egg(s) unattended and on the pore geometry of the shell, which determines the conductance of water vapour. Most water loss occurs between pipping and hatching. Although sulids, cormorants and pelicans incubate eggs beneath or on top of their webs, according to family, the transfer of heat is as effective as in brood-patch incubators and there seem to be no associated physiological peculiarities of pelecaniform eggs.

As top predators, fish-eating birds could be expected to experience post-1947 eggshell thinning due to persistent organo-chlorine residues. Atlantic gannets (20 per cent thinning) and European shags (12 per cent) indeed did so. A 20 per cent thinning is about equivalent to that found in the peregrine falcon at which level a decline in population could be expected. Breeding success of gannets was not monitored anywhere until 1961 but, at least on the Bass Rock, it was very high from then on and the British population increased steadily. By contrast, heavy pollution greatly affected Bonaventure gannets and Floridan brown pelicans. After thinning significantly in the 1960s, the shell thickness of the American white pelican has recovered (Bugden and Evans 1997) and at 0.685 mm is not significantly different from pre-1947—0.683 mm.

Egg shape and colour

Pelecaniform eggs are either elliptical, ovoid or elongated ovoid. They are never round or pear-shaped. Within these forms shape varies, even within species. Because clutches and eggs are usually small, and the webs of cormorants, sulids and pelicans large, incubation, whether beneath or on top of the webs, is rarely difficult. In sulids the limit of this method is reached by the Peruvian booby which may lay four eggs and could not adequately cover more. Some cormorants may lay five or even six but their eggs are smaller and webs larger. The typically elongate eggs of these families may help in this respect since, due to the shape of the webs, the commonest clutches (two or three) are more easily covered than if eggs were round.

Although, except for tropicbirds, all pelecaniform eggs appear to be white, there are differences in the shell colour of newly laid eggs, for example bluish in blue-footed boobies but sometimes pinkish in red-footed. Cormorant eggs are pale blue or greenish white beneath the vaterite whilst those of pelicans are pure white, though coarsely textured. All frigatebird eggs are smooth and white but those of tropicbirds are unique among pelecaniforms, being of a variable background colour (fawn to purplish brown) with speckles or blotches.

Egg fertilization

Sperm storage glands are present in female procellariiforms (Warham 1990), presumably to store sperm from the brief periods when partners are together on the breeding site. It is thus available to be used during the exodus when females are at sea fuelling the egg, which may be laid very shortly after their return. Storage glands are found in auks but are not recorded in pelecaniforms.

Recent years have brought increased understanding of the behavioural and physiological strategies which birds employ to safeguard paternity or, in the case of females, to protect the pair-bond or achieve insemination by the biologically fittest male. Mate-guarding, rape, solicited extra-pair copulations, sperm storage, and sperm competition (Birkhead 1988) are among the phenomena to have gained prominence but, except for the shag, no detailed investigations have been carried out on pelecaniforms (see Chapter 2 and Sp Acc).

Variation in clutch and brood-size between and within pelecaniform families (Figure 3.12)

All cormorants, anhingids and pelicans, and four boobies lay clutches of more than one egg whilst tropicbirds, frigatebirds, gannets and two boobies (red-foot and Abbott's) always lay but one. Pelicans lay two or, in the familiarly aberrant brown, usually three. Cormorants and anhingids usually lay two or three but up to five. Thus within the pelecaniforms more than in any other seabird Order, and particularly in the Sulidae, there is a considerable range in mean clutch-size.

3.12 Clutch and brood-size in pelecaniforms.

<i>Family</i>	<i>Clutch-size</i>		<i>Brood-size</i>		<i>Nature of brood reduction</i>
	<i>Max.</i>	<i>Min.</i>	<i>Max.</i>	<i>Min.</i>	
Pelicans	3(4)	2	3	1	(a) Obligative (early) siblicide (b) Obligative (late) siblicide (c) Facultative siblicide (competitive exclusion)
Gannets/boobies	3(4)	1	4	1	(a) Obligative (early) siblicide (b) Facultative siblicide (competitive exclusion)
Cormorants/shags	4(5)	2	5	1	Only by competitive exclusion, variable stage
Anhinga/darter	6	2	4	2	Only by competitive exclusion; variable stage Mean brood-size \approx 3
Frigatebirds	1	—	1	—	N/A
Tropicbirds	1	—	1	—	N/A

N.B. Bracketed maxima (clutches) refer to rarely recorded figure.

N/A Not applicable.

The relationship between single-egg clutches and tropical, pelagic feeding, as in frigatebirds, tropicbirds and the three pan-tropical boobies (though as single-chick broods rather than clutches) has already been emphasized. Longer foraging trips mean relatively infrequent feeds and hence small broods and slow growth. In this respect pelicans are somewhat intermediate between the pelagic feeders and the inshore feeding cormorants. Often, pelicans forage at a considerable distance from the nest. They lay smaller clutches than cormorants and, unlike them, some species practise obligative brood-reduction early in the cycle.

Within pelecaniform families, clutch and brood-size exhibit a relationship to food similar to that shown between families. Thus the uniquely large clutches and broods of the Peruvian booby are facilitated by the abundant anchovies of the inshore Humboldt, and the blue-footed booby's brood of (sometimes) three by its practice of breeding near to upwelling areas and its mix of inshore and off-shore feeding. Of the three pan-tropical boobies only the red-footed is uniparous but in the other two the brood is reduced to a single chick by siblicide (see below). Although both the red-foot and, particularly, Abbott's booby put more resources into their single egg than the others, the cost in calories of a booby's egg is small—in the case of the

red-foot only approximately 222 kJ (Sotherland and Rahn 1987). Within the time required for egg-formation, the daily investment, of the order of 7.4–24.7 kJ, can be met by less than 4 g of the red-foot's daily catch (Anderson 1980). In view of the substantial contribution to productivity of the second egg in the masked booby, factors additional to nutritional cost must be considered in explanation of the one-egg clutch where it occurs. One such factor may be the danger, in a tree-nesting booby, of the dominant chick falling if it attempted siblicide.

The argument against a two-chick brood in invariable one-egg species relates to the constraints of tropical pelagic foraging. The three gannets may seem anomalous in that although they are not pelagic foragers in impoverished regions they are nevertheless uniparous. However they are exceptional in having followed the stratagem of rapid growth and endowing their single chick with extensive fat deposits, to help it survive unaided transition to independence. (This still leaves the apparent anomaly of the Atlantic gannet's ability to feed extra, donated chicks adequately. Lack's (1954) hypothesis that optimal clutch-size represents the greatest number of fit young that adults can raise without undue stress is rejected by Ydenberg and Bertram (1989) and VanderWerf (1992)

but they cannot take account of the possible effect of rearing more young on lifetime productivity of adults.

Great white, Australian, and pink-backed pelicans rear only a single chick, whilst only a small proportion of American white and Dalmatian pelicans rear two, leaving only the brown and possibly the spot-billed that habitually rear two or more (GFA). The age at which chicks die, or are killed outright by their sibling, varies with species and perhaps with particular populations.

Cormorants resemble pelicans in that there are no uniparous species and individual eggs are notably small. Broods are significantly larger than in any other pelecaniform and mechanisms for brood reduction, although they occur, are decidedly less extreme. No cormorant practises obligative siblicide, and those chicks that die do so as a consequence of competitive exclusion, usually based on size (last hatched are smaller). The same applies to anhingids.

Variation in clutch within species

Clutch-size, or in uniparous species the size of the single egg, is affected by the age/experience of the female and seasonal or annual variations in food. Reliable records of regional differences in clutch-size are difficult to obtain since disturbance, partial predation, counts of incomplete clutches, and the age-structure of the colony can distort the figures. The great white pelican lays smaller clutches in South Africa than elsewhere; Galapagos blue-footed boobies lay smaller clutches than those in California and Peru; European shag and great cormorant clutches vary with region etc. (Sp Acc). Clutch-size generally decreases as the season advances. Even if food is not limiting at the time of laying, the tendency for late offspring to survive less well favours greater investment in early eggs and clutches. The trade-off, however, may be complex; in late clutches individual egg-volume may rise but clutch-size may fall. Also, clutch-size may increase with age of female up to a point and then fall.

The position of the egg in the sequence of laying affects its size and outcome. In the European shag

the first egg is the smallest and the penultimate usually the largest. In large clutches individual eggs are heavier, indicating that the female is heavier and/or a better forager. In cormorants in general, however, individual eggs of larger clutches are smaller than those of small clutches, and egg-dimensions and mass decrease with the order of laying (Cooper 1987).

A valuably detailed study of egg weights within clutches is that of Shaw (1985b) on the South Georgian shag of Signy (Antarctic). Eggs 1 and 2 in clutches of two and of three were similar in volume, but egg 3 could be 4 per cent smaller, giving rise to chicks 8–10 per cent lighter than their siblings; their fate depends on circumstances.

Bigger eggs contain proportionately more albumen, smaller ones proportionately larger yolks. Thus hatchling-size need not be a constant proportion of egg-size. The hatchling great skua represents a higher proportion of small than of large eggs (Furness 1983). Moreover, the degree of asynchrony in hatching is more important than egg-size in determining sibling weight. Stokland and Amundsen (1988) showed that in the European shag hatching asynchrony meant that the first chick weighed on average 1.9 times more than the last to hatch. Although the newly laid first egg had weighed more than the third (the second egg being largest of all) the hatching interval of 60 hours between eggs 1 and 3 was the main cause of the weight difference of chicks 1 and 3. In the South Georgian shag, by the time egg 3 hatched, the chick from egg 1 was already twice as heavy as it and by the latter's fifth day this gap had widened; even chick 2 was twice as heavy. The laying interval is an important breeding adaptation rather than a fixed physiological requirement. Geese, for example, can lay a large egg every day whereas in some pelecaniforms which lay merely two small eggs five or more days may elapse between them.

This staggering of egg-laying and consequently of chick-sizes has four advantages: it gives the female longer to form each egg; it spreads the chick-feeding load on the parents; it allows flexibility in brood-size by providing a ready 'sacrifice' in times of food shortage but provides the opportunity to rear an extra chick under ideal conditions; and it is an insurance policy against failure of the

first egg(s) or chick(s). The insurance is greatest if there is a maximum time difference between first and last egg. Also, if there *is* to be a struggle, it is an advantage to avoid competition between two equally strong chicks. The policy is most valuable where food tends to become abruptly, though often only temporarily, scarce, as in some tropical regions. Long intervals between eggs are practicable only in small clutches, since a large clutch with widely spaced eggs would take too long to hatch.

The mechanism by which laying intervals are increased beyond minimal physiological requirements has not been investigated in pelecaniforms, but ovulation is well documented for albatrosses and penguins. The comparison between black-browed and grey-headed albatrosses (Prince 1985) is particularly interesting because these similarly sized species nest side by side but have evolved different cycle-lengths, in determining which ovulation plays a part. Yolk takes about as long to be deposited in both species, during which period they are at sea, but the lag between the end of yolk-deposition and egg-laying is 12 days in the grey-headed and only 9 in the black-browed. Between return to the colony and laying, the grey-headed has more time to deposit albumen and shell and its egg is 13 per cent heavier than that of the black-browed. A comparable time-lag may be important in those tropical sulids which lay two or more eggs.

Replacement laying

Unlike procellariiforms, pelecaniforms can replace lost clutches depending on how late in the season the clutch had been laid (after the mean laying date in seasonal breeders, clutches tend not to be replaced), how long it had been incubated (half-or-more-incubated eggs tend not to be replaced) and the current state of the food resource. But replacement is an important factor in productivity. Tropicbirds, and especially frigatebirds, are less likely to replace lost eggs. Indeed, in the latter there is no unequivocal evidence for re-laying. Although egg-loss in frigatebirds can be heavy, it is mainly due to conspecific interference, which usually means that the pair-bond has been disrupted and the nest taken over. Similarly in tropicbirds, egg-loss is

often due to usurpation of the nest site, though in this family there is firm evidence for replacement laying. Phillips (1987) recorded 21 per cent re-nesting for the white-tailed tropicbird in the Seychelles after egg-loss and 13 per cent after chick-loss. Stonehouse (1962) recorded re-nesting on Ascension, Fleet (1974) on Kure, and Tyler (1991) on Midway. Even if replacement laying does not occur, the interval between failure and the next breeding attempt may be shorter than between a successful laying and the next one.

Pelicans vary in this respect. Clutches lost in mass desertion obviously are not replaced, but Dalmatian, brown and great white sometimes replace lost clutches whilst American white and Australian pelicans probably do so.

Cormorants may replace lost eggs whether these disappear when the clutch is incomplete or entire. In both cases the birds appear to act as determinant layers. After losing an incomplete clutch they do not lay the remainder at normal laying intervals but start a new clutch after a longer period. Cooper (1987) says of the bank cormorant that no individual female was known to lay more than three eggs to form a single clutch and suggests that all cormorants are similarly determinant.

Atlantic gannets replace most eggs lost early in the season within 5–39 days, usually in about two weeks; some re-lay a second time. Boobies may re-lay after losing egg(s) or chick(s) but with regional and seasonal variation. Kepler (1969) considered re-laying in masked boobies to be of productive importance on Kure but on Tower (Galapagos) and Ascension Island it was not recorded. Similarly, brown boobies on Kure replaced lost clutches in nearly half the cases (Woodward 1972) but few did so on Ascension (Dorward 1962), though Simmons (1967b) by contrast, also on Ascension, found that eggs and clutches at all stages were replaced after, on average, about five weeks. Some pairs laid up to four times after loss.

Replacement-laying may thus be seen as a sensitive means of adjusting productivity to circumstance rather than an all-or-nothing physiological phenomenon. The major pelecaniform exception seems to be the frigatebirds, whose unusual breeding behaviour may make it impracticable.

Incubation

(See Drent 1975.) Incubation can be energetically demanding because in all pelecaniforms except tropicbirds, eggs must be continuously attended, in some species for prolonged shifts. The duration of the incubation period depends mainly on characteristics of the egg such as its mass, mainly yolk-size, though in seabirds, eggs which constitute a larger proportion of female weight do not necessarily require longer incubation. Even within the same family, incubation periods are longer in tropical than in temperate members. For example, the egg of Abbott's booby (about 7 per cent female weight) takes 55 days to hatch whereas that of the Atlantic gannet (same absolute weight as Abbott's but only 3 per cent of female weight) takes 43 days. The egg of the tropical flightless cormorant takes 35 days compared with 29 days for the comparably sized great cormorant. These examples reflect the slow embryonic development of tropical seabirds which, after hatching, continues as adaptively slow chick-growth (e.g. Ricklefs 1979, 1984)). The larger yolk of tropical seabird eggs allows the hatchling to survive long intervals between feeds. Among pelecaniforms, the longest incubation periods (and longest foraging stints) are found in Abbott's booby (57 days), frigatebirds (55 days),

and tropicbirds (up to 51 days). The shortest are in cormorants (as little as 18 days) and pelicans (28 days) and these species forage in short stints. Within each family the range of incubation periods expressed as the difference between longest and shortest as a percentage of longest, is fairly constant at 15–20 per cent (pelicans 15 per cent, gannets and boobies 18 per cent, cormorants 20 per cent, frigatebirds 20 per cent, tropicbirds 18 per cent). Ultimately, the main determinant of long incubation, overriding female body weight, is the species' feeding/foraging regime which influences the rate of embryonic development. Pelagic, tropical foragers require longer incubation stints and incubation periods than inshore feeders.

Incubation is shared and pairs in which partners show markedly disparate incubation patterns fail more often than compatible ones. One partner tends to lose condition and the chick is neglected. Incompatibility increases divorce and this lowers subsequent productivity. Egg-neglect is a facet of brood-reduction; parents give less care to the final egg. American white pelicans selectively neglect the second egg by allowing it to cool after the first has hatched (Evans 1990a, 1990b).

Brood reduction

Where it exceeds one egg, mean clutch-size in pelecaniforms never corresponds to the mean number of young reared by successful breeders.

Neglect of terminal egg

Incubation of the terminal egg of asynchronously hatching clutches may be disrupted by the demands of hatched or hatching eggs. However, in the American white pelican such neglect had no effect on core temperature although it did affect that of the egg surface (Evans 1990a, 1990b). At most, egg-neglect is a minor way of reducing a brood by compromising the last egg.

Siblicidal brood reduction

Competition among siblings may lead to 'facultative' brood reduction, as in the blue-footed booby, Figure 3.14 some cormorants, and some pelicans,



3.13 Siblicide in masked booby. Here, by artificial manipulation, the two chicks were kept alive, but even at this age there was an attempt at eviction.



3.14 Brood reduction in the blue-footed booby is facultative; sometimes two chicks survive. Here the great disparity in size bodes ill for the smaller sibling.

with (in some instances) wounding, malnutrition and death of the younger but it does not inevitably result in the death of all but one chick. In the most extreme case, early and sustained attack by the dominant chick kills its sibling *before* competition for food could be significant, which I called ‘obligative’ siblicide (Figure 3.13) in the masked booby (Nelson 1978b) where only one chick survives. Facultative brood reduction and obligative siblicide are thus importantly different. The former is widespread among birds but, in its most unequivocal form, the latter is much rarer. ‘Obligative’ could be restricted to those species where siblicide by direct aggression, independent of the hunger of the aggressor, occurs always, in all populations and early in the development of the chicks.

Asynchronous hatching facilitates both forms of brood reduction, although opinions differ as to whether this is its main function. Amundsen and Stokland (1988a, 1988b), for the European shag,

concluded, experimentally, that asynchronous hatching (hatching spread 2–8 days) was not adaptive and did not increase breeding success. Fledging success and fledgling weight in asynchronous broods were not higher than in synchronous ones, and brood reduction does not, in general, provide a valid explanation for hatching asynchrony. However, they have no convincing alternative (see also Anderson 1989a; Amundsen and Slagsvold 1990; Ricklefs 1990; Anderson and Ricklefs 1992).

Who benefits from brood reduction—the parents by avoiding stress, the surviving sibling or both? The literature on parent–offspring conflict and brood reduction is now extensive. Key references include: Mock (1984, 1985); Parker and Mock (1987); Anderson (1989a, 1990a, 1990b); Forbes (1990, 1991); Anderson and Ricklefs (1992); Mock and Forbes (1994); and especially relevant to the peleciforms Drummond *et al.* (1986; 1991); Drummond (1987, 1989); Drummond and Chavelas (1989); Evans (1990a, 1990b); Drummond and Osorno (1992); Rodriguez-Girones *et al.* (1996); Drummond and Canales (1998).

In the peleciforms, the most extreme examples of obligative siblicide are the masked and brown boobies and some populations of the great white pelican. As Murphy (1936) and Dorward (1962) reported and Nelson (1968, 1978b), Kepler (1969), Woodward (1972), and Anderson (1989a) confirmed and amplified, the masked booby usually lays clutches of two eggs but hatching asynchrony of some five days helps the first born to kill or displace its newly hatched or tiny sibling. The adult neither restrains the attacker nor aids the victim. In about one-fifth of Kepler’s cases the second egg provided the eventual survivor by being available if the first egg or hatchling disappeared before the second egg hatched (Dorward’s insurance hypothesis), and Anderson confirmed that the second egg had insurance value in all three years of his study (Hood, Galapagos, 1984–86). Is this its sole and necessary function? Is brood size limited by available food (and/or the ability of the adult to tap this resource, combined with the ingestive capacity of the chick) or is there an alternative interpretation of the two-egg clutch and resultant siblicide? Is the masked booby nowadays

capable of raising twins but not doing so? The latter point is amenable to experimentation, although the cost/benefit to the *adult* if it did so, is not (see later).

Nelson (1968) showed experimentally that sibling aggression in the masked booby persists for much longer than natural conditions allow. Similarly Anderson (1990a) tried to determine whether masked boobies were capable of rearing two young if these could be made to coexist, reasoning that, if it could, the one-chick brood may now be sub-optimal. Could the masked booby now rear two chicks were it not for the dominance of the siblicidal allele?

Anderson doubled-up 15 broods before the chicks (all from first-laid eggs and equal in age and size) were a week old. Although nest-mates were mutually aggressive, one of them became dominant and evicted its fellow, but the outcome was thwarted by caging the dominant until weights equalized. Despite this, in only *one* nest did both chicks manage to fledge and even here the chicks were considered to have fledged when they reached 50 days—less than half the actual fledging period. Twins grew more slowly than singletons and each received less food than a normal singleton; their *combined* daily intake at the asymptote was only 325 g against 230 g for a singleton. The adults with twins did not increase their foraging effort beyond that of adults with singletons, although when the chicks were small there had been a hint of such a difference. Indeed when chicks were 20–35 days old, adults with two chicks actually spent *more* time attending them than did those with singles (which, interestingly, meant that twins suffered less from intrusive attacks by non-breeders; one wonders why singles are not attended more).

The result was that from the 15 manipulated broods (30 chicks), 14 chicks reached at least 50 days against 22 from 38 single-chick broods. Out of all the pairs with doubled-up broods only *one* managed to part-rear a set of twins (compare the ease with which Atlantic gannets do so). Is this because the masked booby cannot feed twins or is there a more subtle reason? Although the above result begs important questions and cannot be

taken to indicate that siblicide in the masked booby is maladaptive, Anderson and Ricklefs (1992) nevertheless concluded that obligative siblicide in this booby holds 'realised' brood size below the optimal, despite having earlier (1987) stated that 'the more distant food supply... may be too far from the breeding colony to support the requirements of two chicks'. This latter view is supported by their statement that 'masked boobies *inadequately provisioned artificially twinned broods*' (my emphasis). If they cannot adequately provision twins, how (other than as an insurance policy) can the second egg fulfill a useful function? And if so, when better to jettison the extra burden than early in the life of the brood?. In such a case, the single-chick brood *is* optimal and siblicide *is* adaptive.

Following on from their (1992) conclusion that masked boobies should 'easily be able to provision two chicks at the peak rate', Anderson and Ricklefs suggest that facultative siblicide, as in the blue-footed booby, might have been expected to replace obligative siblicide and has not done so because most masked booby chicks are aggressive; non-aggressive genotypes, they suggest, would almost always be killed by their aggressive sibling.

I suggest that, on the contrary, obligative siblicide is the derived condition and has replaced facultative siblicide (the avian norm) precisely *because* it is an adaptive response to the masked booby's pelagic, blue-water feeding habit. Such foraging entails comparatively infrequent returns with food, availability of which is sometimes erratic. Thus, given the concomitants of this regime, for instance that parental visits may be 'wasted' because the chick cannot cope with the full pay-loads of both parents if these arrive simultaneously and that feeds would often be inadequate for two chicks. There would be periods when two chicks *would* be inadequately fed. The probability that both would fledge underweight (if at all), and with a reduced chance of survival to breeding age, could readily outweigh the occasional apparent gain in productivity.

Adequate computation of cost/benefit would require the longevity and lifetime productivity of adults derived from two-chick broods as against adults derived from singletons, both categories having been reared in the same year (because year-effects

could be significant). Furthermore, the long-term stress on adults of rearing twins could decrease their lifetime breeding frequency. It is virtually impossible that all these facts could be established. The mere survival of chicks to fledging, or even to independence, cannot provide definitive conclusions about the present-day adaptiveness of the one-chick brood.

Finally, there remains the issue of genetic parent/offspring conflict (Anderson 1990b and references). The desideratum is to evolve the brood size which, on average and over the parent's reproductive lifetime, maximizes its contribution to the future gene-pool. If brood reduction increases the probability of one chick surviving in good enough condition to propagate its genes more effectively, over its lifetime, than two chicks would have done, then there is no parent-offspring conflict.

Brood reduction in the blue-footed booby (Sp Acc), which in some regions breeds alongside masked and brown, differs crucially in that siblicide depends on the availability of food. The second chick is comparatively rarely killed outright by its sibling, but is dominated at feeding time, though it may survive until it is well grown and has cost considerable parental investment. Sometimes, two or even three chicks fledge. Thus, in this booby, the option of rearing two or three offspring remains open.

In detailed studies, Drummond and his colleagues (see references) found that the growth of the second chick lagged behind that of the first whether both of them did well or ill; its death, if it occurred, was due to exclusion from food by its hungry older sibling. When the older was experimentally deprived of food and consequently lost 20–25 per cent of its weight, it grew extremely hungry and prevented the junior sibling from feeding. This is precisely why facultative reduction is a flexible mechanism. Guerra and Drummond (1995) demonstrated that second-born chicks do not compete aggressively with first chicks but accept their submissive role (though with a sex bias in favour of male chicks—see below). This concurs with the general observation that an animal's dominance relationships, once accepted, are not repeatedly reviewed. Male chicks survive normally even if they hatch second to their sister and despite being

considerably smaller than females. This appears to be an effect of sex-linked dominance on feeding priority: male sulids are more aggressive within the pair context than females are, and this dominance seems to be expressed even early in development. The Peruvian booby lays two or more eggs, but brood reduction is not usually a feature since there is plenty of food for the entire brood, otherwise, all chicks starve irrespective of brood size.

Among pelicans siblicide as extreme as that of the masked booby has been recorded in the great white (Cooper 1980). In the Dassen Island colony, in every nest with one chick older than three days, the other was dead with extensive head wounds. Even chicks barely capable of lifting their heads attacked their sibling, sometimes before it was clear of the shell. But such extreme behaviour may not be universal in this species. In the pink-backed pelican, which lays two eggs but rears only one chick, most deaths occur between weeks 3 and 9, although some second chicks survive almost to fledging before falling from the nest tree as a consequence of sibling attack (Din and Eltringham 1974a). Such a late death wastes parental investment and it is likely that in a proportion of cases it is the second-born chick which survives. The American white, which in many respects closely resembles the great white, fledges two young per brood in only 20 per cent of successful nests; brood reduction usually occurs in weeks 2–3 as a consequence of severe attacks by the older chick, helped by a hatching asynchrony of 2–5 days (Evans and McMahon 1993 and references). Nevertheless, in 20 per cent of successful nests it *was* the junior chick that survived. Moreover, manipulation of brood-size indicated that the presence of the second chick increased the probability of raising an offspring to the crèche stage from 40 per cent to more than 70 per cent (Cash and Evans 1986). The reasons for this remain obscure. One possibility is that the stimuli received from two chicks encourages the adults to bring more food than they would otherwise have done even if they rear only one. Of the remaining pelicans, aggressive brood reduction occurs in the Australian (Vestjens 1977) and probably the spot-billed (Nagulu 1984), where there is high mortality of the second chick. The brown

pelican is unusual in that although one or two chicks per brood may die and aggression from the dominant chick does occur, some broods of two or even three survive, apparently as a result of a flexible, facultative mechanism. The highest mean number of fledglings from successful nests was 1.6 (Schreiber 1979). In the years when more young fledged per nest, food was more plentiful. Ploger (1997) makes the important point that brown pelicans with experimentally manipulated broods matched deliveries of food to brood size. As a group, therefore, pelicans employ the same brood regulating mechanisms as boobies, except that they all eschew the single-egg clutch. All therefore have an insurance policy.

No cormorant or anhingid is known to practise obligative siblicide although facultative brood reduction is common. The third and/or fourth chick, though rarely the second, dies through inability to compete for food. Thus fewer chicks fledge than hatch and throughout growth there is vigorous competition for food. As in other peleciforms, asynchrony favours the first-born (the Heard shag may be an exception—Sp Acc), and although parents do not interfere directly, casual observation suggests that adults may repeatedly select the chick to feed from two or three equally importunate young. Predictably, third chicks survive better in some years than others. Shaw's (1985a) thorough study of clutch and brood-size in the South Georgian shag showed that although clutches consistently contained three eggs the survival of chicks varied greatly. The third chick, which came from a smaller egg, often starved but second and third chicks sometimes survived equally well. Overall, only 11 per cent of third chicks fledged but if the first or second egg was lost, 71 per cent fledged, though somewhat light. Interestingly, the third chick often starves when the brood's total food requirement is still small compared with the intake of even one large chick. There is much to learn about what controls the amount of food an adult is prepared to gather or yield.

Discussion

Brood reduction raises awkward questions, but in those peleciforms which practise obligative

siblicide the most satisfactory hypothesis for the function of the second egg is insurance, although this fails to account fully for the superior performance of two-egg clutches. (Could these come from more experienced or better-quality females?) Often, the survivor comes from the second egg and even though only one chick survives, clutches of two are more productive than of one. Why, then, do some females of such species lay one-egg clutches? The possible answers (age, current food supply, inevitable variability) seem weak. But clearly the optimum time to 'lose' the second chick, if the first chick is still healthy, is as early as possible. Moreover, even the second chick's genes benefit if, by its own early phenotypic death, genes that would otherwise be lost survive in its sibling. The case of facultative brood reduction does not pose a comparable problem. There the balance of advantage is substantially altered by the greater probability of rearing two or three fit offspring.

Parent-offspring conflict could arise only if the self-interest of the first chick prevents its parents from rearing the second chick when it would have been to their advantage to do so. Then, the elder's genes would be in conflict with those of the parents. Apart from Anderson's finding, cited earlier, that the masked booby can rarely rear two chicks, even to the fledging stage, there is the unambiguous observation that adults make no attempt to control the situation, for example by retrieving a chick, or preventing an attack on it. Thus they do not appear to be in conflict with the first chick. This does not mean that offspring do not attempt to gain food that adults are unwilling to give. A hungry or starving chick exhibits extreme begging and an adult which has tolerated persistent pursuit and pestering, and has already fed the chick, is naturally evasive. But that is not strategic parent/offspring conflict.

The period for which peleciforms feed their offspring ranges from 2 to 18 months, depending on species. The longer an offspring is fed the greater the parental investment and also, perhaps, the greater the curtailment of future reproduction. On the other hand, the greater the investment already made and the greater the cost of wasting it. Such observations warn that any attempt to measure the

costs/benefits of brood reduction experimentally would have to be impracticably long-term and inclusive, taking into account longevity and lifetime productivity both of offspring and parents.

Care of young

(See also Chapter 2.) Except for tropicbirds which are downy and active, pelecaniform hatchlings are helpless and essentially naked. None is able to regulate its body temperature and all require extensive parental care, often well beyond the flying stage. Unlike primary feeders such as pigeons and ducks, pelecaniforms have to acquire special hunting skills

which, with few exceptions, prolongs chick-care (Figure 3.15). Nevertheless, all families except frigatebirds contain species which receive little or no post-fledging feeding.

At first the chick is constantly brooded. After a variable period of guarding which, except in tropicbirds, is rarely less than about three weeks, it may be left unattended. The brevity of the guard phase results in considerable mortality. Among young frigatebirds and pan-tropical boobies attack by conspecific adults, or loss by predation, overheating or chilling can be heavy. Young tropicbirds may be attacked by hole-seeking adults, young pelicans cannibalized, young boobies attacked by

3.15 Some growth parameters in 14 pelecaniforms. (Mainly after Ricklefs 1973.)

<i>Species</i>	<i>Asymptote (g)</i>	<i>Growth rate (K)⁴⁾</i>	<i>Adult weight (g)</i>	<i>Age at first flight (days)</i>	<i>Brood- size</i>	<i>Locality</i>
Brown pelican	4000	0.071	3400 ¹⁾	80	1–3	Florida
Atlantic gannet	4080	0.063	3100	90	1	Scotland
Red-footed booby	900	0.039	1,003 ²⁾	130 ³⁾	1	Galapagos
Masked booby	2000	0.039(?)	1775	113–120+	1	Galapagos
Brown booby	1400	0.060	1300 ²⁾	c. 120	1	Ascension Is.
Abbott's booby	1800?	—	1550	151	1	Christmas Island (Indian ocean)
Double-crested cormorant	1900	0.133	1900	42–49	3–4	Maine
European shag	1600	0.120	1750	c. 60	2–4	England
Great cormorant	2500	0.078	2500	c. 50	2–4	Barents sea
Great frigatebird	1300	0.035	c. 1400	c. 180	1	Pacific (Christmas Is.)
Lesser frigatebird	800	—	806	c. 180?	1	Indian Ocean) (Aldabra)
Ascension frigatebird	1250	0.027	1250	180+	1	Atlantic (Ascension)
Red-billed tropicbird	800	0.060	750	c. 100	1	Atlantic (Ascension)
White-tailed tropicbird	400	0.065	300	c. 80	1	Atlantic (Ascension)
Red-tailed tropicbird	900	0.065	c. 660	c. 80–90	1	Pacific (Christmas Is.)

Notes: 1) Varies with race.

2) Marked difference between sexes.

3) Varies with geographical locality.

4) K is a growth constant indicating the rate at which asymptotic weight is being achieved (Ricklefs 1967a, 1968).

non-breeders. These costs are incurred by the need for both parents to forage simultaneously. This applies less to the inshore feeding cormorants. Uniquely, the Atlantic gannet guards its chick from hatching to fledging.

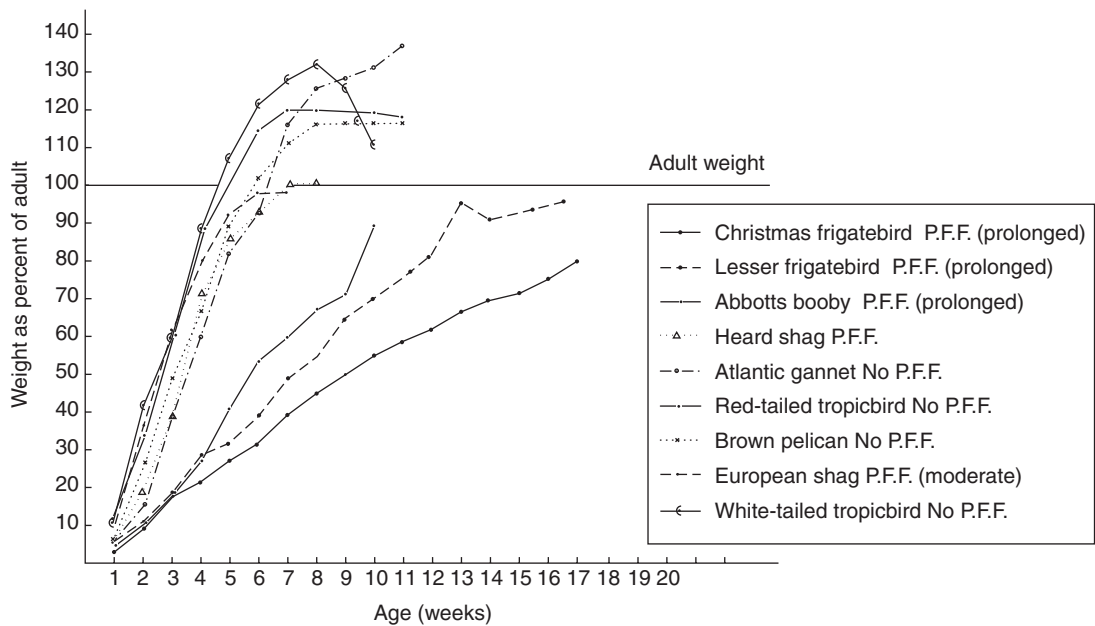
Because some pelecaniform chicks grow much faster than others, irrespective of body-mass, pre-fledging care lasts from less than two months in some cormorants to six months in frigatebirds and Abbott's booby.

In young frigatebirds, tropicbirds, gannets, and some boobies, leaving the actual nest site and acquiring flight occur simultaneously and can be called 'fledging'. But young pelicans, cormorants, and ground-nesting boobies may move from the nest-site before they are fully grown, only gradually acquiring flight. In these cases it is the acquisition of full flight that could be defined as 'fledging'.

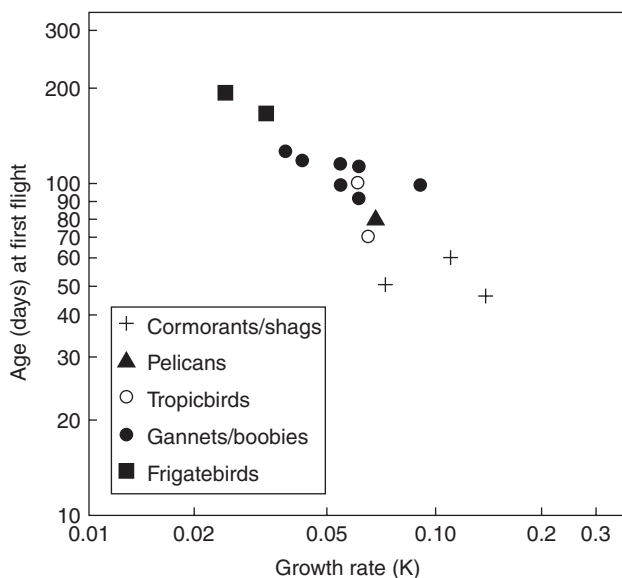
Growth of chick

All pelecaniform parents, like those of other seabirds with altricial young, carry food internally and feed their young by incomplete regurgitation.

The rate of chick growth (Figures 3.16 and 3.17) varies greatly in relation to the species' foraging and climatic regime which determines, also, other aspects of reproduction (clutch-size, deferred breeding, frequency of breeding and longevity). With notable exceptions such as Prince and Ricketts (1981), Croxall *et al.* (1988), Montevecchi *et al.* (1988), Schaffner (1990a), Hamer and Hill (1993), Hamer (1994), and Hamer and Thompson (1997), the effects of the pattern of chick-feeds (the rate and size of meals) on growth have been little studied. Most have focused on average weight of food delivered per day. They have tended to underplay the effect of daily variability in delivery, particularly the intervals between feeds and feed size (Schaffner 1990b found a ninefold range in the masses of individual payloads of white-tailed tropicbirds) and the energy density of the food. Each of these factors could bear on the issue of whether slow growth in seabirds is because adults simply cannot gather more food or is in some way 'optimized'—that is, the parents could provide more food but refrain. Chicks of tropical pelagic seabirds often operate on a 'feast-or-famine' basis, and this,



3.16 Comparative growth rates in pelecaniforms.



3.17 Relationship between age at first flight and growth rate. There is no clear relationship between body weight and precocity (but see Ricklefs for an interpretation linking body size to precocity, using additional taxa). (After Ricklefs 1973.)

irrespective of food abundance at sea at a particular time, imposes severe restraints on growth which has become to some extent genetically controlled. Slow growth is an adaptation to the *likelihood* of food shortage. It may not happen but it may be probable enough over the long term to give slow growth a selective advantage. In that context, it may be unnecessary to look (as does Schreiber 1994) for alternatives to Lack's (1968) hypothesis that slow growth is an adaptation to a (possible) low rate of food delivery.

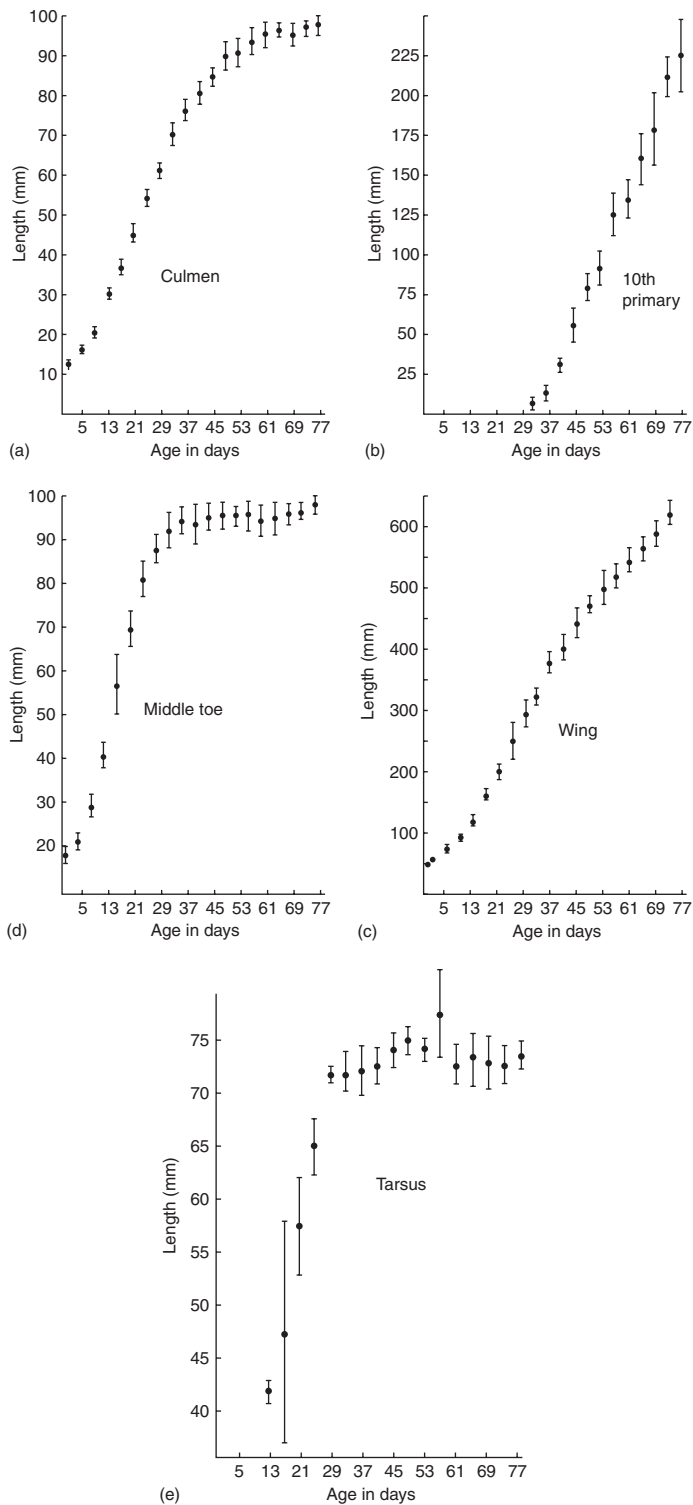
To understand if, and how, payloads are optimized requires documentation of the swallowing capacity (volume constraint) of the chick, the exact time of each feeding, the mass of each payload, the identity of the individual delivering it, and the parents' individual provisioning patterns over several consecutive days (Schaffner 1990a; Sp Acc white-tailed tropicbird).

Growth-rate and brood-size (See also Figures 3.15, 3.16, 3.18 and 3.19)

Of the 62 pelecaniforms, 15 raise only a single chick (seven out of nine sulids, all three tropicbirds, and

all five frigatebirds) and most pelicans produce just one. Two boobies, one or two pelicans, all the cormorants, and the anhingids raise two or more. The single-chick species use a variable growth-rate as their response to environmental fluctuations; the others use a variable brood-size. Apparently paradoxically, the single-chick species grow more slowly than those with two or more, regardless of the weight of the species. Slow growth reflects offshore/pelagic foraging, usually tropical or sub-tropical, whilst rapid growth reflects inshore, usually seasonal/temperate foraging. Even in the same environment, foraging behaviour has a marked effect. For example, the great frigatebirds of the Galapagos take some 130 days to reach a maximum weight of around 1,300 g whereas the Galapagos brown pelican can produce twice that weight in half the time. In temperate waters the great cormorant can produce 7,000 g at a fast growth-rate (Figure 3.15) whilst the Atlantic gannet in the same area takes much longer to produce half the biomass at a slower growth rate, even though, compared with all other sulids, gannet chicks grow rapidly.

These species-typical growth characteristics are geared to ecologically dictated feeding regimes.



3.18 Allometric growth illustrated by the Atlantic gannet. (From Poulin 1968.)

They could not be substantially altered by feeding the young more food. Because of the physiology associated with its slow growth, a young frigatebird can survive longer without food than a young pelican at an equivalent stage. A young Abbott's booby shows extraordinarily slow growth compared even with the red-foot on the same island, itself a pelagic, slow-growing, arboreal booby. Unlike the red-foot, Abbott's has to survive desperately irregular and infrequent feeds during the monsoon period, by which time the red-foot is independent. Abbott's booby's highly adaptive resistance to starvation, inevitably entails slow growth.

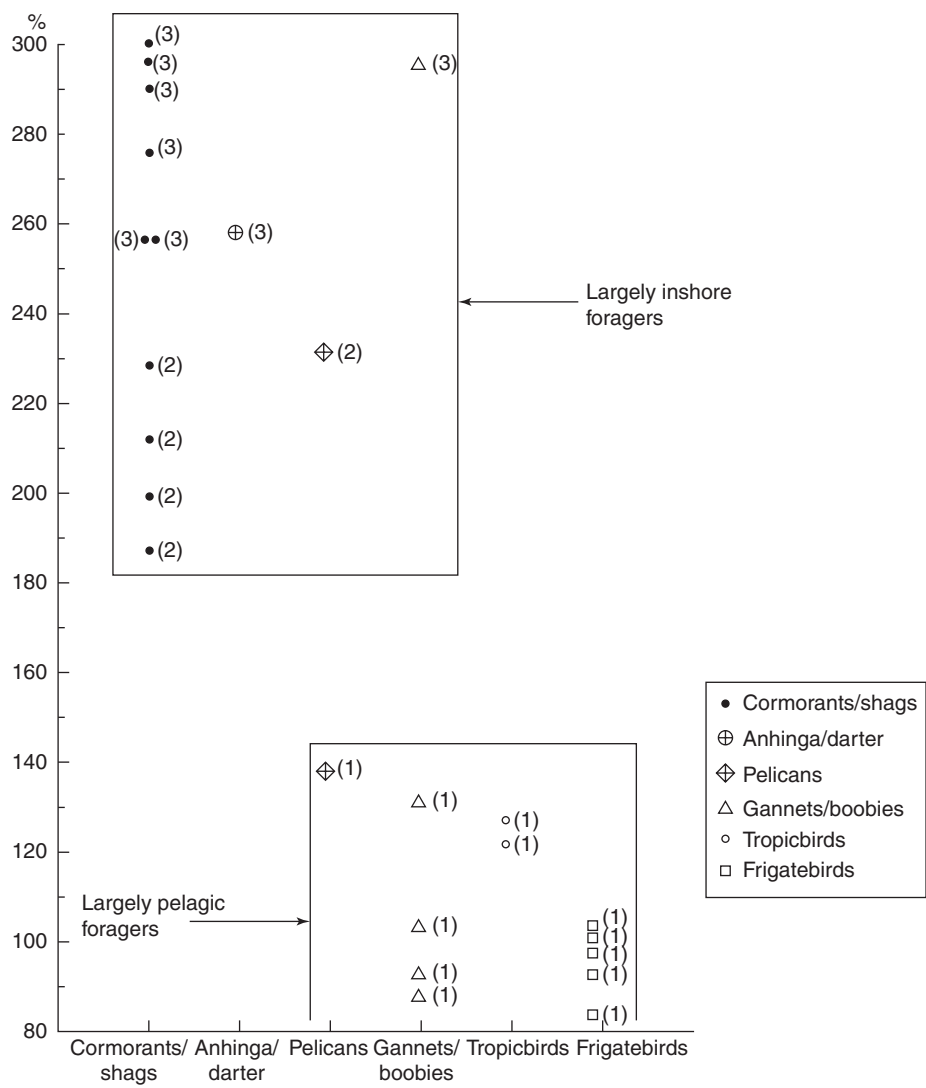
Even within the same species, food-related adaptations in growth-rates are evident. Galapagos red-footed boobies lay larger eggs and grow more slowly than those on Christmas Island (IO) or in the Gulf of California. The magnitude of this difference is shown by their respective growth constants—(K): 0.039 (Galapagos), 0.056 (California) (Ricklefs 1973). He remarks that although the tubenoses, tropicbirds, boobies and frigatebirds all raise single offspring, slowly, this relates to the low mortality experienced by young on oceanic islands, which favours small broods. This suggestion seems questionable since mortality in such species is often extremely high and, even if it wasn't, why should birds raise fewer than they could provided they don't overstress themselves? As Lack (1968) long ago suggested, the main determinant of brood size is how many young the adults can feed adequately. 'Adequately' has to take into account food-loads, frequency, etc.—not solely how much food is 'out there'.

Many seabird chicks, perhaps especially procelariiforms, deposit large amounts of fat. Ricklefs (1979) suggests that prolonged and unpredictable fasting is not the main force acting on selection for such deposits, but that they may be a by-product of diet which, in order to provide all the nutrients required, overprovides on energy-rich components. Subsequently Ricklefs and Schew (1994) proposed that fat deposits may result from raising the *average* feeding rate (thereby overfeeding most chicks) so that the *minimum* rate remains above that which could result in starvation. Nevertheless, it

remains the case that fat is metabolized to provide energy for growth when the intake of food is insufficient to meet this requirement. If parents do not regulate the feeds which they give to their young so as simply to meet current needs, then storage in the form of fat, of temporarily excess food, can act as a buffer against shortfalls.

Parents with broods of more than one can vary the number of offspring which they feed, according to current food. And they can choose which to feed or they can leave this to sibling competition. Although adults do not intervene between competing chicks, they may feed first, second or third selectively. Shaw (1985a) showed that third chicks of the South Georgian shag were highly expendable and second chicks more so than first. Importantly, however, third chicks are adequate competitors once they pass their early period, during which they require so little that food is *not* limiting. Moreover, where third chicks did survive, the growth of first and second was as good as in broods where the third died. The conclusion must be either that, when it died, the first and second had prevented it from feeding or from eliciting parental attention, even when there could have been enough for all, or that the adults withheld food. That tiny first and second chicks, at a time of plenty, would sometimes prevent their third sibling from feeding but at other times would not (since it doesn't always happen), when in any case the third was not going to affect their own growth, makes no sense. In theory they should act early, as in obligative brood reduction, or wait until (if ever) current shortage of food dictated reduction as the optimal procedure, 'remembering' that survival of siblings increases their own inclusive fitness provided the cost is low enough.

The mean weight of feeds increased thirtyfold between days 1–10 and day 40. Yet it was in the early period that third chicks died, when broods of three ate only a tenth as much as older broods of two. However, from the behavioural viewpoint, one cannot assume that parents *could* bring in as much food to small chicks as, later, they do for large ones. Small chicks present a specific set of sensory stimuli—vocalizations, appearance, movements—and the adults forage as an innate response to that



3.19 The approximate maximum biomass (percent adult weight) reared by pelecyaniforms. Brood size in brackets.

combination. The larger feeds brought in for big chicks are a response to *their* behaviour. It may not be possible to exchange the two sets of responses. If, for whatever reason, the foraging in response to small chicks provides less food than they need, then the third chick suffers. Anderson and Ricklefs (1992) similarly suggested that parents do not, or cannot, interpret the chick's begging in relation to their nutritional needs. This implies that adults are programmed to reduce the likelihood of manipula-

tion by chicks. As a (largely rejected) alternative hypothesis, group-selection (Wynne-Edwards 1986) would suggest that the adult's decision to feed the third chick rests on assessment of resources and current levels of exploitation.

Patterns of growth

(Figures 3.15–3.19.) During development the chick uses energy in an adaptive, species-specific

way (Ricklefs 1968, 1979, 1984; Dunn 1980; Montevecchi and Porter 1980). Food fuels tissue-growth (muscles, organs, bones) and activity. Different parts of the body grow at different rates which suit the species' particular requirements. Digestive efficiency increases as the gut grows. Thus a steadily decreasing proportion of the chick's weight is due to viscera whilst more is attributable to appendages, muscles and feathers. The shape of the growth curve varies with species (see Figure 3.16). Frigatebirds increase most rapidly early in growth, reaching the point of inflection (the point at which the absolute rate of growth begins to decrease) when less than a third of total growth has been achieved. Then, during its most demanding phases, it grows more slowly, adapted to the comparatively small and infrequent feeds decreed by the adults' mode of foraging. In cormorants and gannets the point of inflection is reached later in growth, even though they require considerably more food than frigatebirds.

Energy is used to control body temperature, for basal metabolism and for exercising, preening, begging and other behaviour. In the double-crested cormorant about 38 per cent of 'existence' energy expenditure goes into temperature-regulation (Dunn 1975). This is likely to be near the figure for other altricial pelecaniforms and illustrates the great advantage enjoyed by the semi-precocial, hole-nesting tropicbird which can thermo-regulate within a day or two. Gannet chicks are unable to maintain a constant body temperature until they are 15–18 days old (Montevecchi and Porter 1980). However, adults are able to attend them continuously throughout their entire period in the nest. In strong contrast, many tropical pelecaniforms take longer to achieve homiothermy and yet adults cannot afford to attend them for more than the minimum period, since both parents are required for food-gathering.

The energy from food of a given calorific value depends on digestive efficiency. This is higher in fish-eaters than seed or insect-eaters, and so less energy is lost in excreta. The calorific value of the food given to young fish-eaters may change throughout the nestling period, which may imply complex feeding adaptations by parents. Moreover,

the efficiency with which these different foods can be digested ranges, according to the chick's gut-development, from 30–85 per cent. Intestine length changes during growth and is itself highly and positively correlated with metabolic rate (Bech and Ostness 1999). There is ample scope for differences between individual parents in providing the most appropriate food from the prey-spectrum at each stage of development, an ability which may require experience (see Age of First Breeding). The increased foraging effort required of parents as their chicks grow increases their own consumption, which imposes an additional burden on them. Growth is discussed in Ricklefs (1968, 1973, 1984), Dunn (1975, 1980), Montevecchi and Porter (1980); Montevecchi *et al.* (1984), O'Connor (1984, 1985).

Except for tropicbirds, the pelecaniform hatching may weigh less than 2 per cent of the adult. Yet adults are large or very large, and this biomass is rapidly achieved by the chick even in broods of 2, 3, or 4. This trait is typical of birds that hunt prey for their offspring, which are usually altricial and grow much faster than precocial young, which find their own food. A brown pelican's fortyfold increase during its first eight weeks, expressed as the growth constant (K), is 0.071, which is similar to that of altricial landbirds of comparable size. K is affected by several variables and differs both within and between pelecaniform families and even within the same species in different localities (Ricklefs *et al.* 1984). Blue-footed boobies in the Galapagos reach the phase of rapid growth about 10 days later than in Peru (Duffy and Ricklefs 1981), whilst the growth of the tarsus is delayed by up to three weeks. Even within the Galapagos archipelago itself there are significant differences. Comparisons made at one time may show a different pattern from those made at another. The growth of the blue-footed booby ($K = 0.062$ – 0.066) compares with an estimated 0.039, 0.052 and 0.056 for the more pelagic red-footed booby and 0.060, 0.094 for the masked booby.

The marked differences between figures for the same species presumably reflect locality or seasonal differences. Cormorants tend to grow more rapidly despite their larger brood ($K = 0.078$ – 0.208 ,

double-crested cormorant). Rapid growth is possible because of the large volumes of nutritious food that fish-eaters can provide. This builds on the high proportion of embryonic tissue present in altricial hatchlings. But for the first two days growth depends on the remains of the yolk, which contributes almost a fifth of the hatchling's weight and is an important adaptation (see The Egg).

The pelecaniform chick consists largely of water, plus fat, protein and minerals, the relative proportions of which, and thus the energy available to the chick, change during development. The 'energy density' of the chick (roughly its nutritional health) depends on its food, hence the importance of quality as well as quantity. For example, the energy density of the Atlantic gannet increased with age, up to 9 weeks (which is about the time of maximum weight), mainly because of the accumulation of fat (Nelson 1978a, Montevecchi *et al.* 1984). A key factor in this is the prominence of mackerel in the diet after the first two or three weeks. Montevecchi *et al.* calculated from captive chicks that during the 13 weeks in the nest a young gannet consumes some 24,000 g of food, providing 190,550 kJ (a measure of available energy). Of this, about 45,550 kJ are lost in excreta, leaving 145,000 kJ for growth, maintenance, temperature regulation and activity. The chick's intake increases rapidly up to six weeks then decreases slightly and levels off. The changes in food intake coincide with changes in growth and activity. The efficiency with which the chick utilizes food can be gauged by the amount of fat deposited. Gannets appear to be similar to other piscivores and of the same order as most passerines (Montevecchi *et al.* 1984 and references). Their especially large fat deposits are effectively a substitute for post-fledging feeding. Ultimately, the Atlantic gannet's system has evolved under climatic selection pressure which favours early fledging and migration.

In all seabirds, growth is strongly allometric; bill, wings and legs grow at different rates (Figure 3.18.) The particular pattern, as in the gannet's fat deposits, is adapted to the requirements of the species during growth and after fledging. Cormorants grow faster than other pelecaniforms but their asymptotic

weight is always less than adult weight. In general, only species with post-fledging feeding can afford to fledge without at any stage having exceeded adult weight.

Post-fledging parental care

Pelecaniforms, in complete contrast, for example, to albatrosses, shearwaters, petrels, and penguins, tend to prolong the feeding of free-flying offspring. Young seabirds are likely to survive better if they are fed during the transition period but in theory the cost to parents may decrease their breeding life. The cost/benefit balance is not known for any pelecaniform. One may, however, look at the occurrence and extent of post-fledging feeding in relation to lifestyle. Burger (1980) tables its presence or absence in various groups (though mistakenly attributes it to albatrosses). Within the pelecaniforms, frigatebirds have by far the longest periods whilst the Atlantic gannet has none. In between there is everything from six months in Abbott's booby (including the difficult monsoon period), two to eight or more weeks in cormorants (less in anhingids), a variable period or mostly none at all in pelicans, a variable period but usually a month or more in the other boobies. Very probably there is none in tropicbirds.

This wide range in parental investment is a further instance of the many different ways in which species use available resources. The fledgling Atlantic gannet's fat deposits make it too heavy to fly once it has landed on the sea; it cannot return to be fed. Nor would it be logistically practicable for its parents to feed it at sea. Providing it with fat stores in lieu of post-fledging feeding maximizes the adults' use of seasonally abundant food and expedites the fledglings' southward migration which post-fledging feeding would delay. All other sulids show post-fledging feeding, most prolonged in the tropical, pelagic feeders.

Factors relevant to the duration of post-fledging feeding in the pelecaniforms include the difficulty of acquiring foraging skills in relation to climate and the nature of the food resource. Frigatebirds and tropical boobies have the longest post-fledging feeding. They use a demanding feeding method

and their food resources can be thinly dispersed, patchy and unpredictable. The fledgling thus finds it hard to feed itself. Even after several months of post-fledging feeding some Galapagos juvenile great frigatebirds starved to death (Nelson 1968), though that was an ENSO year. Similarly Abbott's booby, with greatly extended post-fledging feeding, faces exceptional hardship (Sp Acc). It seems that the duration of post-fledging feeding is longer in the more 'difficult' regions and in the more pelagic sulids.

In cormorants, post-fledging feeding seems essentially pragmatic. Free-flying young can frequent sea-rocks or colony environs and practise fishing between feeds from their parents, who rarely forage far away. Thus post-fledging feeding can be finely adjusted to the availability of local prey and, even within a species, is highly variable. It lasts longest in the flightless cormorant (Galapagos) but in this instance is part of a special adaptive web (Sp Acc). Apparently no cormorant entirely lacks it.

In pelicans post-fledging feeding is restricted or absent. Some may be fed after their first flight if they remain near the colony. Pink-backed pelicans, which nest in trees, feed their free-flying young at the nest or in trees some distance away (Burke and Brown 1970). Brown pelicans may feed free-flying young but the duration seems variable (Schreiber 1976a). It is likely that great white pelicans become independent soon after they can fly. Brown and Urban (1969) say 'apparently the young leave the colony as soon as they can fly and never return until fully adult' and 'once the young have left the colony we have never seen any indication of feeding by adults, nor do the young solicit food from adults'. Where the breeding colony is adjacent to water, as it usually is, well-grown young pelicans may practise fishing for themselves before they are fully fledged, thus reducing the need for post-fledging feeding.

Once the young tropicbirds have flown out to sea they do not return (GFA). They fledge with some fat reserves which could sustain them until they acquire fishing skills. Adults do not accompany them at sea (the difficulty of maintaining prolonged contact in such a solitary and far-foraging species

would be considerable). Sightings at sea of solitary young are rare but although adult/young duos have been noted, feedings have not. Yet, in their transition to independence, tropicbirds face similar difficulties to frigatebirds and tropical boobies.

As pelecaniform chicks grow, their begging becomes more vigorous, often frenzied. Adults no longer initiate feeding, as they often do in the early stages; instead, they become progressively more resistant. After Trivers (1974), this is interpreted as conflict between the demands of the young and the advantage to the parents of restricting further investment. This can be a difficult assessment. When a juvenile great frigatebird dies because its parents stop feeding it they lose a heavy investment, possibly for the sake of a little further support. Recalling the severe demands which breeding makes on frigatebirds, and the long recuperative period which follows, it seems maladaptive to abandon support at this point. However, once parents have reached the upper limit of a pre-programmed period of post-fledging feeding they may be unable to assess the juvenile's chances of survival. These problems, common in seabird biology, can be resolved, if at all, only by impractically long-term research of a kind yet to be done for any species.

Post-breeding attendance

As soon as their young become independent, most adult pelecaniforms disperse to moult and recuperate. None is known to accompany its young either to sea or on migration. Gannets, especially the Atlantic, appear to be the sole exceptions by remaining on-site for a prolonged period of intense territorial and pair-bonding behaviour. Many pelecaniform colonies are active all year because new individuals replace those which have departed, as in some tropicbird colonies, some tropical boobies, and some African colonies of great white pelicans. After breeding, several cormorants and some boobies attend the colony for roosting and loafing but territorial behaviour is desultory or absent. Frigatebirds and tropicbirds are not known to frequent the colony after successful breeding but detection would depend on prolonged study of marked individuals.

Other Aspects of Breeding

Breeding success and productivity (Figure 3.20)

Pelecaniform species differ markedly in the various components of breeding success (hatching, fledging and post-fledging survival). Some are more vulnerable than others to predation and disturbance and to food shortage. Within a species, other factors, such as age and experience and colony size may affect breeding success, defined as young fledged from eggs laid ('reared to independence' would be more meaningful but less practicable). Considered as the number of young fledged per pair per breeding attempt, the families in descending order are: anhingids (around 3), cormorants (around 2.0 but in some species around 3), pelicans (around 1.0), tropicbirds (0.3–0.5), and frigatebirds (0.1–0.5). The sulids vary so much (0.1–2.0+) that some are as modestly productive as frigatebirds whilst others equal the output of cormorants. Both between families and within the sulids it is the marine inshore, or estuarine or (except sulids) freshwater feeders which produce most fledged young, in line with their greater clutch-size and faster growth. Predictably, those families and species with the greatest geographical range, and thus the widest extremes of climate and food, show the greatest variation in breeding success.

Some pelicans are so sensitive to disturbance that figures for breeding success are often meaningless. Schreiber (1976a) warns that comparison of productivity obtained by different workers using different methods and in different years are untrustworthy. This caveat should be heeded, especially by seabird biologists using these figures in complex models. This apart, they seem fairly similar, achieving on average slightly less than one chick per pair. Hatching success can be more than 90 per cent and breeding success around 50 per cent. Historically, pelicans have probably enjoyed consistent and high breeding success over most of their extensive range but are now seriously affected by loss of habitat and disturbance. The *Pelecanidae* is by far the most threatened family in the Order.

The enormous differences in sulid breeding success can be more readily related to climate and food.

The breeding success of the three gannets, especially the Atlantic, is two or three times that of most boobies; though, because they lack post-fledging feeding, young gannets must suffer higher post-fledging mortality. Their high fledging success results from plentiful, reliable food, often in contrast to the pan-tropical boobies. Within species, as in the Atlantic gannet, there may be great consistency between regions or, as in the red-footed booby, considerable differences. In the Caribbean and on Kure Atoll the red-foot achieves a breeding success of 70 per cent or more compared with (often) less than half that in the Galapagos where 90 per cent of eggs laid may fail to produce fledged young. Brown booby breeding success on Christmas Island (IO) was 65 per cent compared with less than half that figure on Ascension. Similar differences apply to masked and blue-footed boobies in different regions. In the Peruvian, success varies not by region but between years. Normally it is extremely high but in ENSO years it can be zero.

Despite a wider distribution and variety of feeding habitats than any other pelecaniform, the marine inshore and inland-water feeding habit of cormorants is such a determining influence that, except the flightless cormorant, they all lay clutches of two to four eggs and rear two or three young. Nevertheless, in most species there is regional and between-year variability in success. Mass desertion can occur when food becomes scarce, as, for example, in Cape, guanay, great and flightless cormorants. Even in sub-Antarctic and temperate northern regions, breeding success fluctuates. For example, in the European shag on Lundy, fledging success is normally 90 per cent, but in some years is only around 60 per cent (Snow 1963). In South Georgian shags on Signy it may be more than 80 per cent or only half that figure (Shaw 1985a).

Anhingids are probably the most productive members of the Order with the least tendency to experience crash years or massive non-breeding.

Frigatebirds vary little in form, size, feeding or social behaviour. Nevertheless, differences in breeding success occur between species and populations. Some populations, for example of the great frigatebird in the Galapagos, seem particularly prone to loss through conspecific interference. Starvation seems

3.20 Estimates of lifetime productivity in some pelecaniforms.

<i>Species</i>	<i>Young fledged per breeding attempt</i>	<i>Estimated breeding attempts per lifetime</i>	<i>Young fledged per lifetime</i>	<i>Comment</i>
Great white pelican	0.8	9	7.0	Enormous variation between localities and years
Brown pelican	1.0+	7	7+	Sometimes raises two young; experience of adults important
Atlantic gannet	0.75	15	11.0	Highly consistent between regions and years
Abbott's booby	0.3–0.5	15+?	4.5–7.5	Periodic catastrophes (monsoons); biennial breeding and interposition of non-breeding years—means breeding life-span longer than other sulids
Blue-footed booby	0.5–1.0+	8–10	4.0–10+	Little information on adult mortality/longevity. Considerable regional variation in productivity and breeding frequency
Great cormorant	2.0–2.5	7	14.0–17.5	Human interference vitiates widespread comparisons but typical productivity high compared with other pelecaniform families
Galapagos cormorant	0.5	8.5 (male) 15.0 (female)	4.3 7.5	Female begins new cycle whilst male feeds fledged young. Unless sex-ratio skewed at birth, or adult mortality rates unequal, adult sex-ratio should be skewed
South Georgian shag	2–3	6	12–18	Estimate of breeding attempts extremely approx.
Great frigatebird	0.5 or less	10	5	Biennial breeding and non-breeding years indicate extremely long lifespan, though adult mortality rates remain to be determined
Red-tailed tropicbird	0.4+	10–12	4.4–5.3+	Breeding success variable; lifetime productivity probably higher than indicated here

N.B. Local variations considerable.

the major cause of failure. Yet, even on the same island (Aldabra), over the same period and feeding on much the same prey, both in type and size (Diamond 1975a), the great frigatebird achieved 51.4 per cent breeding success and the lesser only 13 per cent (Reville 1980). But one may not assume that, elsewhere, lessers achieve only 13 per cent nor that this low figure is typical for Aldabra.

Assessing lifetime productivity in frigatebirds is particularly difficult. They take an unknown number of non-breeding periods, of unknown duration; disturbance effects are incalculable; regional and yearly differences in success are not known.

Like frigatebirds, tropicbirds form a small, close-knit family, all feeding in the same manner. Their breeding success is higher than that of frigatebirds, possibly because they are less vulnerable to disturbance *en masse* and to interference from conspecifics. Also, their preferred nesting habitat affords greater protection from weather and predators. They compete for nest sites and it seems anomalous that on Ascension, where such competition is severe, chicks were guarded less than on Cousin (Seychelles) but suffered lower mortality (55 per cent chick loss in the first 15 days compared with 71 per cent on Cousin).

Other than food, the most important causes of failure in most pelecaniforms are man-induced, either directly or by the introduction of pests or predators (Chapter 4). Avian predators are never a major threat. Sea-eagles in Norway take shags, but these form less than 1 per cent of prey items. There are many examples of limited depredations by predators or scavengers, such as several species of gulls and corvids, and of raptors such as short-eared owls, Galapagos hawks, turkey vultures, on the eggs and chicks of boobies, frigatebirds, cormorants, and even pelicans, but all affect small numbers. The Polynesian rat can in some years cause total nesting failure of red-tailed tropicbirds and kill even adult white-tailed tropicbirds (Schreiber and Schreiber 1993). Compared with massive natural predation, as on terns, auks, and petrels, these pelecaniform examples are insignificant.

Age of first breeding (Figure 3.21)

This ranges from 1 to more than 10 years. This is a major and little understood aspect of seabird biology

(see for example Coulson 1966; Nelson 1970, 1990; Carrick 1972; Mills 1973; Harrington 1974; Ainley 1975; Fisher 1975; Ollason and Dunnett 1978; Ryder 1980). To achieve maximum productivity a seabird 'should' breed as soon as it is well nourished, physiologically mature, competent in foraging, local 'lore', and social behaviour, and able to secure a site. These parameters may be impossible to quantify but comparative studies provide some insight. Long-deferred breeding in seabirds does not correlate with the size and weight of a species, nor with type of nesting habitat, colony size or density or social complexity. Nor is there a clear correlation with feeding mode such as surface snatching, pursuit-swimming, plunge-diving or other, although, possibly, plunge-diving and surface-snatching take longer to acquire. However, breeding tends to be longer-deferred in far-foraging than inshore-feeding seabirds. Within the pelecaniforms, frigatebirds require longest (probably 7–11 years) and pelicans and cormorants least (commonly only 2 years). Sulids breed for the first time between 3 and 6 years and tropicbirds at 3 to 5.

Several studies indicate that prey-catching improves with age but it is not clear why. In plunge-divers, after a comparatively short period during which physical coordination is perfected, the assessment of feeding opportunities probably becomes the most important factor. Even if the execution of the dive is perfect, faulty assessment of the chances of success will reduce capture rate. The peregrine falcon's stoop can be acquired in time to breed at little over a year, so it is unlikely that lack of physical skill will detain a seabird for five years or more. 'Feeding lore' (knowing where to feed) could be crucial for a seabird to feed adequately under the constraints of operating from a fixed base—the breeding colony. This entails learning how to recognize potential feeding areas (maybe subtle visual cues), where best to forage under different weather conditions, and the acquisition of a memory 'bank' as a result of past foraging, all of which is likely to be more demanding in pelagic than inshore feeders. Trans-oceanic yachtsmen graphically describe dramatic transitions in weather and sea conditions, and probably therefore in food.

It is difficult to forage from a fixed base. Fisher (1975) showed that the Laysan albatross suffered

3.21 Deferred breeding in pelecaniforms.

<i>Duration of deferred breeding</i>	<i>Pelicans</i>	<i>Gannets/ boobies</i>	<i>Cormorants/ shags</i>	<i>Anhinga/ darter</i>	<i>Frigatebirds</i>	<i>Tropicbirds</i>
Less than two years	Rarely; occasionally brown pelican and pink-backed	Occasionally Peruvian booby; possibly blue-footed	Several cormorants/ shags breed in 2nd year	Probably common	None	Rare; can occur white-tailed
2–4	Most individuals, all species	All except Abbott's can breed	All, or almost all others	Probably all others	None	Probably most individuals all 3 spp.
4–5	Probably a few Dalmatian great white American white	Most gannets, some red- footed, some Abbott's	Rarely, if any	None	None	Probably a few, all 3 spp.
5–6	Rarely, if any	Some Abbott's, some red- footed, some gannets	None	None	Probably none	Probably rare
More than six years	None	Probably some Abbott's	None	None	All	Probably none

1. Strong correlation between inshore fishing and short period of deferred breeding.
2. Short period deferred breeding correlates with short fledging period.
3. Information rarely quantitative.

only adult-rate mortality two years after fledging. But in the first site-attached year (even though they did not breed), erstwhile nomads were compelled to operate from the colony in time-limited foraging spells. Consequently, mortality due to starvation rose again. Similarly, Carrick and Ingham (1967) suggested that the wandering albatross may need 10 years to perfect its ability to forage from a fixed base. The recent studies of Weimerskirch *et al.* (1988, 1992, 1993, 1994a, 1994b), Weimerskirch (1992), Weimerskirch and Wilson 1992, Weimerskirch and Robertson (1994), show how extensive and region-specific these foraging trips are.

Ainley (1975) suggests that delayed breeding in the Adelie penguin may be due to immature social behaviour. Whilst this 'explanation' ignores ques-

tions such as sex-differences at the age of first breeding, it draws attention to the role of social behaviour. Unfortunately there are few objective criteria for ranking social complexity. Species with extremely simple displays, such as the fulmar, may show deferred breeding periods three or four times as long as those, such as cormorants, with extensive and highly ritualized repertoires. Although behavioural development can be related to age, as shown by Harrington (1974) for the sooty tern and Ainley for the Adelie penguin, it can scarcely explain the differences between species; neither can competition for a site, which in any case could apply only where they are physically or socially limited.

In some species males and in others females breed first. Feeding proficiency is unlikely to explain this.

However, in the Atlantic gannet, pre-breeding feeding opportunities are more curtailed in the male because he assumes a disproportionate role in site attendance and defence. Whether or not for this reason, males breeding for the first time are older than females (Nelson 1976). In some seabird species the time spent guarding the site and the energy invested in display is greater in males but never in females. Indirect evidence for greater stress in males is their higher mortality, as in red-billed gulls (Mills 1973) and kittiwakes (Coulson and Wooller 1976). Contrary to the stress prediction, however, and to the case of the Atlantic gannet, in both these gulls males breed when younger than females. Moreover, the male red-billed gull assumes the extra burden of feeding the female during courtship. However, in these gulls the females lay comparatively costly clutches. But the female Atlantic gannet can easily afford its small egg and breeds when younger than the male. However, the trade-off in each case must be complex.

Deferred breeding together with long life, single-chick broods, slow growth, and relatively infrequent breeding relate to pelagic as against inshore feeding. Flexibility in the timing of first breeding permits individual differences in fitness, or perhaps even density-dependent differences between populations in relation to their food resource, to be accommodated within the framework of achieving optimal lifetime productivity. This major function may account for its ubiquity and for the enormous differences between and within species.

Breeding success in seabirds is higher in older, experienced birds than in first breeders (see Ryder 1980; Nelson 1990; Wooller *et al.* 1990). Detailed evidence comes from gulls, fulmars, albatrosses, shearwaters, and penguins, but the principles probably apply to most pelecaniforms. Wooller *et al.* concluded that in short-tailed shearwaters reproductive performance was influenced by age, cumulative breeding experience, and the better survival of successful breeders. Brooke (1978a) found much the same for the Manx shearwater and implicated experience as particularly important. Older birds perform better for several reasons. Some innate behaviour patterns such as incubation and care of the newly-hatched chick are inadequate in some young, inexperienced birds who neglect their eggs

and incubate poorly. Gannets may ignore or displace a newly laid egg or crush a hatchling by failing to transfer it from beneath the webs. Several workers have noted for a variety of species that some parents, presumably inexperienced, have difficulty in feeding the new chick. Some behaviour patterns are under hormonal control and develop over a latency period which varies between individuals and may not be fully ready when first needed. Finally, experienced breeders may be better foragers.

Older birds have pair-relationships which are more fully compatible, and they are more prone to retain their mate of the previous year. They are therefore more effective breeders; they lay earlier and are more successful. In the short-tailed shearwater (Bradley *et al.* 1990) half of all males and females had only one breeding partner during their lifetime. In both sexes, 74 per cent retained their mate of the previous year. The later in life the bond was formed, the longer it lasted. Breeding success was greater among pairs whose bonds lasted longer. The 'mate factor' can be so strong that, if partnering a new male, regardless of his age, female red-billed gulls with several years of breeding experience reverted to laying close to the date of first-time breeders and suffered reduced success (Mills 1973).

The evidence that young parents might be less adequate providers is conflicting. Whilst Atlantic gannets and Manx shearwaters provision their young adequately, Laysan albatrosses breeding for the first time suffer increased mortality and may be presumed to be less adequate providers (Fisher 1975). Yet the weight of first-time breeding fulmars was greater than that of experienced birds, perhaps suggesting that they were giving less to their young (but see Hamer and Thompson 1997). In the South Georgian shag, females aged 6–12 kept their third chicks alive almost twice as long as females aged 3–5 (Shaw 1985a). And older females tended to hatch their chicks more synchronously, which reduces their mortality.

Non-breeding years

Circumstantial evidence suggests that there are years during which experienced pelecaniform adults with

surviving partners nevertheless do not attempt to breed. Non-breeding, adult-plumaged individuals are present in considerable, sometimes huge, numbers in many seabird colonies, including gulls, skuas, auks, penguins, petrels, shearwaters, fulmars, albatrosses, and many sulids, frigates, and tropicbirds; perhaps less evidently in pelicans and most cormorants. In different years the proportion of non-breeders ranges widely—in pelagic cormorants of the Semidi Islands (North Pacific) from 0–80 per cent (Hobson 1997). The length and frequency of non-breeding periods within an individual's lifetime are not known for any pelecaniform. Apart from pre-breeders, the fitness status of non-breeders with previous breeding experience is always unknown. Evidence from other Orders seems conflicting. Ainley (1975) demonstrated that some Adelie penguins of good weight and with adequate gonads did not attempt to breed. But Carrick (1972) demonstrated an apparent threshold weight for newly arrived royal penguins below which they did not attempt to breed. In some seabirds adult weight and breeding success are positively correlated. The inference that in low-weight individuals the reproductive reward would not outweigh the cost implies that the avoidance of stress is important. Thus frigatebirds, Abbott's boobies, and red-footed boobies not only take years out but even when breeding they appear to maintain their own condition whilst not infrequently allowing their chicks to starve (Nelson 1969, 1976, 1978b). But in large-brood species with generally high productivity, stress and the associated reduction in lifespan may conceivably be outweighed by short-term productivity. Kortlandt (1940) notes that breeding great cormorants appeared severely stressed. Such species may be expected to breed when below optimum weight whereas longer-lived ones with single-chick broods and a lower productivity may not do so. This largely corresponds to the contrast between inshore feeders in seasonal, temperate regions and tropical pelagic feeders.

The simplest suggestion seems to be that non-breeding is a response to the level of the food resource. Klomp and Furness (1992), for the great skua on Foula, relate both a decrease in the number of breeders and a sharp drop in breeding suc-

cess to a decrease in sand-eels. They support the conclusion of Porter and Coulson (1987) that the number of non-breeders at seabird colonies may provide an early and sensitive indication of environmental changes adversely affecting the population, and that non-breeders buffer such stress. In the presence of abundant food every mature and fit individual could be expected to attempt to breed. Yet even in successful breeding populations, as in many Atlantic gannetries, there are (sometimes many) non-breeders although their level of fitness is not known. If, as Wynne-Edwards (1986) proposed, such apparent restraint can operate on the basis of *individual selection*, benefiting the future of the *group* of which the non-breeding individual is itself a benefiting part, then non-breeding could aid optimal utilization of resources.

The energy which it is advantageous for an individual to invest in a single breeding attempt depends on interacting factors, including adult life expectancy, mortality before first breeding, capacity of female to modify brood-size in response to fluctuations in food, and the rapidity with which adults can regain lost condition. The complexity is well illustrated by the kittiwake, where central-site males breeding for the first time at four years old arrive later, lay later, father smaller clutches but nevertheless rear more young than centre-site males breeding for the first time at five years. But they survive less well during the two subsequent years than do males which first breed at five (Wooller and Coulson 1977).

Great frigatebirds in the Galapagos may refrain from breeding for one or more years after a successful attempt. Abbott's booby takes years out, as does the masked booby, another tropical pelagic feeder with a single-chick brood. Woodward (1972) recorded 20 birds of this species that bred one year, returned the following year as did their partners, but did not breed. By contrast, during a 10-year span, none of my individually-recognizable pairs of Atlantic gannets failed to attempt to breed.

The many adult-plumaged non-breeders in seabird colonies thus pose important questions. It is unlikely that all can be physiologically or nutritionally inadequate, so why aren't they breeding? Whatever their state, they can cause disruption among breeders.

Attacks on unattended chicks by (probably males) of their own species have been noted in frigatebirds, tropicbirds, masked boobies, Australasian and Atlantic gannets, several pelican species, and great cormorants, and are doubtless widespread. It is unlikely that its function is to disrupt breeding and thereby release experienced females into the pool of potential mates. Unless sites are limited and there is serious imbalance in the sex ratio, there is no obvious reason why fit non-breeders should not form pairs from the available pool without interfering with established breeders. And the high probability is that in many cases, sites are *not* limited, and females are available.

Social aspects

The consistency with which seabirds breed at species-specific densities suggests either the evolution of maximum density due to site shortage or some advantage accruing from the observed density. But it is difficult to relate breeding success to density. Many other things, such as edge/centre effects and parent quality affect success. At most, the effect of density is slight and imprecise except (though not in pelecaniforms) for its anti-predator function. The same is true of colony size. Small colonies of species which usually breed in large ones do tend to have lower success, as Bempton gannets did when the colony was small (Nelson 1978a), but once the colony provides adequate social interactions and contains a normal proportion of experienced breeders, size seems not to affect success.

The failure of newly independent young to acquire feeding skills counts as breeding failure since parental genes have not been passed on. However, it is not parental failure except insofar as parental investment may (as it transpires) have been prematurely withdrawn. Perhaps genetically viable young will achieve adequate skills after the normal period of parental subsidy, and the failures (as they turn out to be) would, on average, have been poor risks for further investment.

Abandonment of breeding

Some pelecaniforms desert eggs or chicks during food shortage, but in temperate, seasonal latitudes,

wholesale desertion of undisturbed colonies is rare or unknown. But tropical, opportunistic breeders such as some populations of red-footed boobies may desert during a food shortage (Nelson 1969). Temporary shortages have to be survived without undue stress on adults and desertion of clutch or brood is then adaptive. It is more important to conserve long-lived adults than to produce one or two extra chicks, few of which survive to breed. Mass desertion sometimes occurs in the opportunistically breeding pelicans and also in those cormorants, pelicans and boobies whose large, dense populations depend on local super-productive upwellings, which occasionally fail.

Longevity and mortality

Meaningful breeding success is achieved only when offspring breed or help kin to do so. Indeed, birds that fail to breed may handicap their local population by uselessly competing for food or disrupting breeders. In pelecaniforms, as in most seabirds, annual mortality of pre-breeders greatly exceeds that of adults. Presumably, the acquisition of the skills required for locating and catching prey prove too difficult, particularly during adverse weather or when food is scarce. After the first year, during which, presumably, the physical aspects of hunting are perfected, mortality is not highly age-specific, but in first-year pelecaniforms it seems typically of the order of 60–75 per cent. Young seabirds are less efficient foragers than adults and it seems adaptive that they should disperse widely. Most pelecaniforms, except the flightless cormorant, some endemic sub-Antarctic shags and perhaps some of the lesser known freshwater cormorants, migrate or disperse once they have become independent. Nomadism largely removes them from competition with adults and conserves energy by eliminating return to a fixed point, thus allowing maximum utilization of patchy food.

Comparatively few adult mortality rates (Sp Acc) have been accurately determined since they depend on the reliable return of individually marked adults to a known breeding place and on the durability of the marker. Mortality must be lowest in those species with the lowest productivity, namely

frigatebirds and Abbott's booby, followed by some other boobies and the tropicbirds, and then by pelicans and cormorants. For example, if 20 per cent of eggs laid by frigatebirds survive to breeding age—a generous assumption—it would require a pair of breeding adults to live for 20 years, breeding once every two years, to replace themselves. Since they take rest-periods of at least one year between successive, successful breedings, their average breeding lifespan is more likely to be 30 years or more, which means annual adult mortality would be 3.3 per cent. Abbott's booby, too, must live at least 30 years (Sp Acc). This figure is close to those of the large albatrosses and it emphasizes how important it is that such long-lived, low producers should not be killed by man if populations are to remain stable.

By contrast pelicans, cormorants, and anHINGIDS may be expected to have a considerably shorter expectation of breeding life, perhaps less than 10 years.

Summary

1. Current peleciform numbers are in general not limited by lack of breeding habitat. Exceptions may be some populations of tropicbirds and, increasingly, some European populations of pelicans.
2. Colonial breeding is discussed and summarized.
3. The timing and frequency of breeding in peleciforms exemplifies almost every possible option, from almost continuous readiness to be triggered, through strictly annual, seasonal cycles to loosely seasonal annual or biennial ones.
4. Pre-laying attendance is highly variable. Some cormorants, especially endemics, may attend the breeding area continuously, if sporadically, but the norm in the Order is for a fairly short pre-laying attendance. Only in some pelicans and cormorants is it shorter than three weeks.
5. The incubation period, as a part of the developmental process which continues in the chick, is related to feeding/foraging regimes and is longest in the pelagic, tropical peleciforms, especially frigatebirds and Abbott's booby.

6. Except for the semi-precocial tropicbirds, all peleciform chicks are altricial. The period of chick brooding and guarding varies with species but is never less than the period required for the young to be able to regulate their own body temperature (at least 3 weeks). Thereafter, chick-guarding is related to the need for both parents to forage simultaneously. Only Atlantic gannets show full-time attendance between hatching and fledging. Pelican chicks, and those of some cormorants, form crèches, primarily as devices to control body temperature.
7. Post-fledging parental care ranges from none (the three gannets, some pelicans and probably the tropicbirds) to more than six months (frigatebirds and Abbott's booby). These differences are discussed.
8. Post-breeding attendance at the breeding site is brief or absent in most peleciforms but prolonged in the gannets where, especially in the Atlantic, site-defence is important.
9. Peleciform eggs are discussed in relation to their size, composition, and shells.
10. Variation in clutch and brood-size is discussed particularly in relation to brood reduction (facultative versus obligative siblicide). Both methods are adaptations to achieve optimal brood-size but under different sets of circumstances. Obligative brood reduction is here considered to be the specialist (derived) condition and facultative reduction the avian norm. Obligative siblicide in its most extreme form occurs in the masked and brown boobies and in at least some populations of great white and American white pelicans. In such species the second egg is an insurance policy. The largest clutches and broods occur in the cormorants where they relate to inshore and/or freshwater feeding.
11. Most peleciform species replace lost eggs or chicks under certain circumstances, but replacement laying has not been unequivocally demonstrated for frigatebirds and is probably rare in Abbott's booby.
12. Chick-growth patterns are discussed in relation to feeding/foraging patterns and brood-size. The relationship between first, second, and third chicks is described.

13. There is wide variation in breeding success and productivity between and within pelecaniiform species. Frigatebirds experience the lowest success and productivity, whilst cormorants have the highest productivity, though not the highest breeding success. The greatest differential between the highest breeding success/productivity and the lowest is found within the Sulidae.
14. Age of first breeding varies from (probably) 5–11 years in frigatebirds to (sometimes) less than 2 years in cormorants and possibly in some pelicans.
15. Experienced breeders take ‘rest’ years in frigatebirds, some sulids, probably tropicbirds, but are less likely in pelicans and cormorants.
16. Mortality, especially between independence and first breeding, is notoriously difficult to ascertain. Adult annual mortality is assessable for some species and probably ranges from just over 3 per cent (frigatebirds and Abbott’s booby) to perhaps 15 per cent (some cormorants).

Pelecaniforms and man

Introduction

Pelecaniforms face the same formidable problems as many other seabirds and, like them, require active management based on legislation and education, global databases and monitoring, and coordinated international research (see Nettleship 1991; Nettleship and Duffy 1992). Technology offers powerful new tools not only for following the activities of the birds themselves but for modelling population dynamics and the interactions between seabirds and fisheries, and much else. Unfortunately we lack the most basic information: the numbers of the commoner and widespread seabirds. We know only that they are decreasing.

Pelecaniforms have engaged man's imagination, entered his literature and art, and been exploited in various ways perhaps more than any other group of seabirds. But man's main impact has been to reduce the range and numbers of many species and drive some to extinction. Steadman's (1989) contention that species-extinction on a massive scale has been brought about by man applies forcibly to waterbirds. Today, many are threatened by the loss or degradation of habitat, especially wetlands important for pelicans and cormorants; Canada has lost three-quarters of her wetlands and in parts of Europe the situation is even worse. The crucial reservoir of great and Dalmatian pelicans in Russia faces severe loss of habitat. The Pantanal in Brazil, one of the world's largest wetlands, is threatened by pollution, exploitation, deforestation, expanding agriculture, and unplanned tourism (Alho and Vieira 1997). An ongoing assessment of the world's wetlands is now becoming feasible through Satellite Remote Sensing

and an associated model (HAM or Habitat Available Model) (Tatu *et al.* 1999).

There has been enormous loss of marine food resources, massively increased disturbance (the importance of which can hardly be exaggerated), pollution by persistent toxic chemicals, by oil, and by synthetic discards such as netting, line and plastic waste. In some albatrosses, though not pelecaniforms, casualties on a scale which threaten the survival of species have resulted from modern fishing methods such as drift nets and long-line fishing. 'Today more seabirds are killed annually during commercial fishing in the North Pacific than by all other human activities in Alaska combined' (Kondratyev 1995). In addition there has been massive destruction by introduced predators, and in some cases by killing for food or because of perceived but often misinterpreted conflict of interests between man and bird. Often, protection is not merely inadequate, it is entirely lacking. In Manitoba fishermen illegally kill thousands of double-crested cormorants whilst Ontario protects cormorants and views them as indicators of chemical pollution in the Great Lakes—living litmus paper (Keith 1995).

Many seabird colonies are sensitive to disturbance at much greater distance than commonly supposed (Erwin 1989). Gotmark (1992) provides a detailed critique of disturbance caused by research work. Then there is the effect of unrecorded disturbance (D.W. Anderson 1988) which vitiates breeding biology studies and for which there is no remedy except constant surveillance. General remarks can easily fail to do justice to its calamitous effects. More than 20 years ago Anderson *et al.* (1978) recorded disturbance to seabird colonies by

tourists (including guided ones), fishermen, egg-collectors, scientists and educational tour groups *in five consecutive years* in some study areas, and things have since become worse. These disturbances can lead to total failure in productivity as a consequence of desertion, loss of eggs to predators, overheating of eggs and of chicks. These authors point out that predation by gulls, for example, does not occur in the absence of human disturbance; certainly true of herring gull predation on gannet eggs (Nelson 1986). Klein *et al.* (1995) analyse some aspects of the deleterious effects of ecotourism and suggest some partial solutions, whilst Rodgers and Smith (1995) and Yorio and Quintana (1996) analyse the response of colonial waterbirds to the variable proximity of humans. The latter observed a site occupied by five seabird species and proposed as a tourist area. Disturbance led to considerable loss of eggs, although birds became less wary as the season advanced. A minimum distance of around 25 m between observers and birds was essential.

Little wonder, then, that the plight of seabirds causes grave concern. And now there is the threat of global warming leading to the inundation of low-lying habitat of marine peleciforms, and the unprecedented disruption of major oceanographic phenomena such as the Gulf Stream.

On the brighter side, efforts are afoot to construct adequate databases, to model population trends and interactions with fisheries, and to improve cooperation between seabird biologists and between their discipline and others. There is a need to raise public awareness of current threats and to promote International Marine Reserves which, to be at all effective, must often go beyond the 320-km territorial limit. In addition we need International Treaties on the avoidance of oil pollution. Management and Conservation should be based on an improved understanding of seabirds at sea, which has always lagged far behind our knowledge of their breeding biology. As Nettleship and Duffy (1992) conclude, large-scale cooperative projects must be set up to identify and protect important breeding areas (for example, by pest control and wardening), to protect foraging areas, to reduce or eliminate pollution, to control fishing levels, and to devise sound models for assessing and then managing seabird

populations. A tall order indeed. Cairns (1992) provides a cogent assessment of the possible role of seabirds in improving the models which fishery biologists use to assess fish stocks. From the fishery point of view he, too, strongly commends collaboration with the 'newly minted discipline of avian marine ecology'.

As an example of a practical advance, in this instance for assessing the vulnerability of seabirds to surface pollutants, principally oil, the information collected by several nations since 1980 has been combined to form the European Seabirds at Sea Database, which for some areas gives seabird density (birds/km) for several species. This database holds more than a million records, giving sightings of more than 12,500,000 seabirds. It makes possible an Atlas of Oil Vulnerability within the North Sea which can be used by ships to avoid sensitive areas. Using seabirds to monitor the marine environment, both in connection with fish stocks and as indicators of pollution such as oil, heavy metals and organochlorines is vitally important (e.g. Furness and Camphuysen 1997). The Pacific Ocean Biological Survey Programme (POBSP) has amassed huge amounts of information on the breeding populations, movements, and occurrence at sea of many tropical seabirds including the three booby species, two frigatebirds, and two tropicbirds. Much of this remains to be published. PIROP (Programme Intègre des Recherches sur les Oiseaux Pelagiques) provides a unique database of seabird observations from the entire eastern Canadian coast, 1966–92 in relation to oceanographic data. It is now possible to carry out spatial analyses using GIS (Geographical Information Systems) (Huttmann and Lock 1997).

On the legislative front, international agreements are urgently needed. The Bonn Convention supposedly covers migratory birds, which include many peleciforms, but is widely ignored. The African/Eurasian Waterbird Agreement (AEWA), April 1994, stipulates effective conservation of waterfowl and their habitats. Species to be preserved include some, like the great cormorant, which are in many countries routinely killed as pests. AEWA is intended to function as the governmental platform for the integrated conservation and management of

the entire western palaearctic flyway. Protected species will include several pelicans and many cormorants. Birdlife International is currently developing a plan to conserve the world's seabirds, including the development of a colony database.

Species-studies will continue to help conservation by establishing mortality and recruitment rates (there are excellent examples in Nettleship *et al.* 1994) but increasingly the need will be for syntheses, decision-facilitating databanks and cooperative ventures (Nettleship and Duffy 1992).

In essence, managing seabirds means managing their breeding habitat, including control of pests and disturbance and the regulation of fisheries. Tatu *et al.* (1999) have developed a technique (satellite remote sensing) for measuring wetland habitat. For an exhaustive review of the status and problems of seabirds over much of the world see the splendid Technical Publications of the International Council for Bird Preservation (ICBP) (Croxall *et al.* 1984; Croxall 1991).

Methodology

Whilst there is no substitute for asking the right questions, recent advances in technology have made it possible to obtain answers formerly beyond reach. Important amongst these are devices which can be attached to, or swallowed by, the bird and which can record and transmit or store information of various kinds. Many pelecaniforms are robust enough to bear the attachment of electronic recording instruments or data loggers. These may be radio transmitters attached to the bird, for example to the ventral surface of tail feathers, or to a leg, or to a harness which enables them to lie flat along the bird's back. Transmitters can send signals back to land-based receivers, perhaps via satellite, which follow the bird's course at sea. Exciting work by Weimerskirch *et al.* (1993) in detailing the extraordinary foraging journeys of the breeding wandering albatross could scarcely have been dreamt of a few years ago. Global locating sensors record light intensity at dusk and dawn in a particular wavelength, storing data for use after the instrument has been recovered. This allows the bird's position at sea to be determined (two fixes every 36 hours), is

smaller and cheaper than satellite transmitters, and is able to store data for incredibly long periods of up to two years. They have already been used on penguins and albatrosses and seem to have enormous potential for elucidating the wandering or migratory movements of seabirds outside the breeding season. The main problem seems to be attaching the device securely, in a position where it can receive the appropriate light signals and where it can remain for an extended period without inconveniencing the bird. As Wilson *et al.* (1986) have emphasized, however, the effect on a bird's subsequent behaviour of handling, attaching, and recovering devices is an important unknown which is always ignored. Also, on smaller birds such as white-tailed tropicbirds, a transmitter makes the bird use more energy (Pennycuik *et al.* 1990). Miniature water-temperature loggers can be attached to a leg and linked to position-determining devices which can reveal features of each foraging trip including (for penguins) swimming speed and heading and dive depth. For other large seabirds they can record the time spent in flight or resting on water, and the sea-surface temperature in the bird's foraging area (Wilson *et al.* 1995). Stomach-temperature loggers are carried internally after being fed in a fish to captured birds, and record each fall in stomach temperature as an item of prey is ingested. Devices which measure the timing, depth and duration of dives have been successful on shags, and together with measurements of flight direction and distance are of great value in determining the location and hence, perhaps, the characteristics of the feeding areas.

Recent work (Hamer *et al.* 2000; Lewis *et al.* 2001) on Atlantic gannets, using satellite telemetry, has provided fascinating information on the direction and distance of foraging trips, which has allowed (for example) the correlation between colony-size and foraging distance to be postulated.

A Geographical Information System can be used in conjunction with information on diving behaviour and feeding rates when fishing at different distances from the colony, in different depths and over different bottoms (Wanless *et al.* 1997a, 1997b). Simple activity recorders—digital watches with external electrodes that short-circuit if immersed in

seawater—have been devised by Cairns *et al.* (1987) to record flying time. Depth gauges attached to the backs of Adelie penguins record time spent underwater and depth of dives (Wilson *et al.* 1991). Use of doubly labelled water (DLW) to measure energy consumption in free-living seabirds (see Birt-Friesen *et al.* 1987) has refined estimates of energy used and food required, with obvious benefit for modelling food consumption and its relation to commercial fishing. Keller (1997) used DLW to investigate daily energy expenditure of wild cormorants but his work involved first, drugged bait (alphachloralose) to catch them, and then shooting them for the final blood sample which, to the cormorant, might have seemed excessive. Ballance (1995) used DLW in conjunction with activity recorders to monitor the energetics of flight and foraging behaviour of red-footed boobies. Bevan *et al.* (1997), for the South Georgian shag, used an implanted data logger to record continuously the heart rate and abdominal temperature, and a time-depth recorder to monitor diving behaviour.

Automatic nest balances in conjunction with radio-tracking systems (Gremillet 1997) can provide detailed information on foraging and feeding efficiency and gross daily food intake. Great cormorants were shown to be extremely efficient predators with a median catch of 15.2 g of fish per minute spent under water.

Feather analysis (ratio of carbon and nitrogen isotopes) can be used to determine the extent of freshwater as against marine feeding (Bearhop *et al.* 1999). It has shown that freshwater feeding is extremely important in, for example, the great cormorant and has increased in recent years.

Molecular marking techniques can reveal relatedness within and between colonies, indicating the extent of gene-flow and, for example, foraging overlap. Siegel-Causey (1997) used molecular analysis of the present genetic structure of rock shags to indicate that a formerly continuous population was separated, by glaciation, into discrete populations where they remained without contact for some 20,000 years. Afterwards, populations recolonized and mixed in the central part of the present-day range.

Time-lapse photography is a non-intrusive method of recording a whole raft of behaviour and ecology, such as attendance stints, incubation behaviour, chick feeding frequency, interactive behaviour and much else. Video-recording and the transmission of images to reception centres for analysis has immense ethological potential. The problems are mainly practical, such as cost, adequate housing of cameras in the field, protection from human interference, positioning the camera (as in the case of treetop recordings of Abbott's booby's long-term behaviour) etc.

From the sublime to the ridiculous, it is often necessary to catch adult seabirds to attach rings, tags, transmitters, etc. For large birds like pelecaniforms it is simple to use a telescopic pole and padded loop, opened and closed by the operator. Kuiken *et al.* (1997) describe an ingenious system which enabled them to capture pelicans and double-crested cormorants without disturbing the colony, whilst Bowman *et al.* (1994) used night-lighting. Disturbance was minimal and there was no gull predation. Similar techniques have been used to capture roosting cormorants (King *et al.* 1994). A variant has been successful on double-crested cormorants from a boat, using a long handled net. At close quarters birds may be marked with paint or dye applied via pellets, using a blowpipe or other means such as felt-tips attached to fibreglass rods. Even small marks are sufficient and where it is impossible to catch them or disturbance is unacceptable, this expedient can be vital. Reville (1980) used it on groups of displaying frigatebirds, gaining valuable information on individual behaviour. Individual identification can be variously achieved; a modern method uses implanted micro-chips.

It might appear that the day of the field naturalist, with binoculars, notebook, and simple devices, is past, but nothing substitutes for direct, intimate observation.

Seabirds, food and populations

Because man's activities hugely affect fish and therefore seabirds, communication and cooperation between numerate seabird and fishery biologists will be essential. For example, at present,

crude assumptions about the effect of the seabird catch on the amount available for fishermen are universally accepted and are probably wrong. Nor are the estimates of what seabirds take likely to be accurate. For example, calculations of consumption can be wildly adrift if models are based on inaccurate estimates of metabolic rates, especially costs for thermo-regulation and flight (see Birt-Friesen *et al.* 1989). The direct approach, multiplying the weight of fish caught per day by each bird, by the size of the population, and calculating the proportion of the fish stock which this figure represents, is also fraught with error and provides highly inconsistent conclusions. Nevertheless, Furness and Cooper (1982) calculated that in the Saldanha Bay fishing area, jackass penguins, Cape cormorants and African gannets (93% of the total South African breeding seabird population) consumed fish representing nearly one third of the mean annual commercial catch. Other studies, too, have indicated that seabirds, predatory demersal fish, and industrial fisheries are in direct competition. But, considering seabird consumption of sand-eels in relation to industrial fishing in the North Sea, Furness and Tasker (1997) conclude that seabirds take only about 4% of the stock and that fisheries have far greater potential to affect seabirds than the converse. Nettleship (1991) and Nettleship and Duffy (1992) point out that fishery managers need procedures to decide whether there is a real conflict between them and seabirds, as some ecological energetics models would suggest. Similar 'decision trees', incidentally, could address the impact of tourism and management options.

Meanwhile the serious decline in world fish stocks accelerates. Fishing vessels of several nations now comb the remotest areas of the world's oceans, including equatorial belts formerly unexploited because their fish densities were uneconomical. Large, predatory fish such as tuna have been massively exploited and this can be expected to affect those seabirds such as frigatebirds and boobies which benefit from the game fish driving flying fish to the surface where they become accessible. There is hardly an important fishery worldwide which has not declined significantly in the last 30 years and whether we consider herring in the North

Sea, sand-eels, mackerel, saithe, cod, anchovies, sardines, sprats, squid or whatever, the story is the same. Whilst it is impossible, in most cases, to relate the fluctuations in seabird populations and productivity directly to human exploitation of a particular fish species, the very scale of the fishery effort, for example in removing more than a million tons of sand-eels from one small part of the North Sea each year, is almost certain to affect those seabirds which depend on them. As remarked above, the need is for adequate cooperation between seabird biologists and fishery scientists to gather the information and do the predictive modelling.

Commercial fish-farmers have real grounds for complaint about birds. Aqua-culturists with artificially high densities of fish can lose, for example, 20–25% of production in carp-rearing ponds—see Keller *et al.* (1996) for Bavarian carp farming. Here, the vexed issue concerns the methods by which the losses can be prevented. By decreasing the density at which fish are stocked, predation greatly decreases (halving density results in nearly a fourfold decrease in predation). But fish farmers require a high density! Keller (1996) reviews control techniques, including crossed wires to prevent landing, enclosure systems, and various forms of disturbance.

Where large inland waters are stocked for sport fishing, for example trout in Loch Leven (Scotland), the amount that cormorants caught did not affect that caught by anglers (Carss *et al.* 1997), nor did killing cormorants help anglers to catch more fish, and in 1994 killing was discontinued as a form of management. In Sweden, Engstrom (1997) attempted to discover whether there were fewer perch and roach near to a large cormorant colony than further away. He found no such decrease in abundance within a radius of 10 km from the colony.

The position is complicated in those seabirds, including most pelecaniforms, which exploit many species, switching from their preferred prey to other kinds. Whilst the effect of reduction of preferred prey species may be masked for a time, the seabird's productivity over the longer term is likely to be affected. Switching to less-preferred prey may involve changing foraging habits, perhaps travelling further or modifying feeding technique, such as dive-frequency or depth, and the duration of fishing

stints. Any such change will affect breeding biology but in subtle ways which only detailed investigation could reveal.

Fish are not the only problem. The weight of cephalopods landed worldwide has also increased dramatically from a million tons in 1970 to 2.7 m in 1989–92, mainly in the SE Pacific and SW Atlantic (Boyle and Boletzky 1996). Many seabirds depend on cephalopods (see Croxall and Prince 1996).

The role of the huge amounts of discards by commercial fishing may be important in the food economy of some seabirds (see, for example, Garthe *et al.* 1996) but probably has little significance for any pelecaniform species, though it could be a factor in the increase of the Atlantic gannet.

A few fishery biologists are interested in seabird population trends, for example in gannets and cormorants, and in breeding success and changes in diet as possible indicators of available fish stocks (Crawford and Shelton 1978, 1981; Newman and Crawford 1979; Burger and Cooper 1982; Hockey *et al.* 1983). Intensive commercial fishing such as purse-seining and demersal trawling now appears to be the greatest single threat to populations of some seabirds. More than 95% of seabirds off South Africa and Namibia are Cape cormorants, African gannets, and jackass penguins. Burger and Cooper (1982 note that 'the overall abundance of certain populations of prey has been reduced by fishing ... while the proportions of prey species and the size of fish available have been altered. This has co-incided with notable changes in the population sizes and diets of some species of seabirds'. Bank and crowned cormorants seem unaffected by the fishing industry.

Adequate censuses of breeding seabird populations remain of central importance. Fry (1992) points out that truly massive kills of seabirds at sea have sometimes been assumed, against all common sense, to have had little effect on breeding populations, as though birds were phytoplankton! This apparent ability to absorb vast losses may well be because distant breeding populations have not been adequately censused and declines have gone unnoticed. Also, many species have a substantial buffer of non-breeders which, however, can become seriously depleted with, presumably, catastrophic effects on breeding populations at a later date. The

low productivity and low capacity for recovery after catastrophe is masked in many seabirds by their long life; numbers take a long time to fall noticeably. Thus a species' population size at a particular instant may not be an adequate reflection of its health. To decide whether or not it is in trouble requires the incorporation of all relevant data into a predictive model.

The history of seabirds in relation to introduced pests is long and universally calamitous and the general facts are too well known to need repeating. A single illustration will suffice. Baker Island, some 3,000 km SW of Hawaii, is only about 145 ha and 6 m high. Cats, introduced by the US Airforce, eliminated the seabirds. In 1964 the cats were removed by the POBSP and by 1978 there were at least 10,000 sooty terns, more than 1,000 brown noddies, 600 masked boobies, 8,600 lesser frigatebirds, and smaller numbers of several more species (Forsell 1982).

Poaching, made easier by powerful outboard motors, is an extremely serious threat on innumerable tropical islands. It is difficult to counter; general attitudes often favour it; political and conservational will and resources are inadequate.

Many seabird breeding haunts attract thousands of visitors; from Newfoundland to Scotland and New Zealand via the Gulf of California, the Galapagos, the Falklands, and Antarctica. Whilst popular interest in and concern for seabirds is much to be desired, tourist disturbance can be a threat. A new way of bringing seabirds to people is via constant-surveillance cameras remote from the viewing centre. These convey live pictures of life within the colony and the technique has enormous educational and research potential. In Brittany cameras operate in the gannetry on Rouzic whilst the Scottish Seabird Centre in North Berwick (Scotland) receives viewer-controlled pictures from the Bass Rock, Fidra, and the Isle of May.

Pelecaniforms and the past

Pelicans

With their unmistakable anatomy and pouch, pelicans are prominent in folklore. The Greek 'pelekys',

meaning axe, somehow gave rise to pelekton and then, in English, referred specifically to this group of birds although previously more widely applied. 'Pelecanus' implies, also, a shovel. More obscurely, the Spanish 'alcatraz' is derived from the Greek 'kados' (water pot). The Hebrew 'kaath', meaning to vomit, is readily explicable given the pelican's method of feeding its young by regurgitation. Although Pliny's 'onocrotalus' resembles in many respects a pelican, as suggested by 'there is a kind of second belly in the very jaws. Herein, the insatiable animal crams everything at once', it is nevertheless generally assumed to be the bittern (Evans's edition of Turner, 1544).

The dove may be the most pervasive symbol of piety but the pelican, because of its supposedly self-sacrificial nature, is prominent in ecclesiastical heraldry and carvings. On the badge of the Guild of Corpus Christi the pelican appears above a nest containing its young (Alexander 1953). It is used in the Arms of Richard Foxe, Bishop of Winchester, and is part of the heraldry of Christchurch which Foxe founded in 1515. Del Hoyo *et al.* (1992) recount the Indian fable of the pelican who treated her young so roughly that she killed them (pelicans do treat them extremely harshly). Remorsefully, she then drew blood from her own breast and, with it, resuscitated them. This is a recurrent association, probably because pelicans rest the bill tip on the breast and (Dalmatian) have a blood-red pouch early in breeding. In medieval art the pelican commonly symbolizes mercy. In Pakistan it symbolizes peace, though it is incorporated into the heraldry of the 60th Punjab Regiment. Like the gannet, the pelican symbolizes gluttony and, like the gaudy booby, it is reckoned to be foolish. King Lear refers to his daughters as 'pelicans' to portray their ingratitude and, by implication, his own suffering.

Like gannet fat, that of the pelican has been valued as an embrocation. Their pouches make containers and their skin and feathers have other domestic uses. Eggs and young have been eaten but pelicans have never been as systematically exploited as gannets, perhaps because they are tough and fishy.

Although inferior to guanay cormorants and Peruvian boobies as a source of guano (Hutchinson

1950), the Chilean race of the brown pelican was one of the 'big three' producers on the Peruvian guano islands, especially the Lobos Islands and, earlier, the Chinchas. Indian villagers use the droppings of the spot-billed pelican as fertilizer and African villagers collect spilt fish from beneath the nests of pink-backed pelicans. Pakistanis reportedly use tethered pelicans as decoys and pelican skins as camouflage beneath which to approach other aquatic birds.

Gannets/boobies

The vernacular name 'gannet' is both generic and specific. Like 'gander' it means 'goose' (see Nelson 1978a). The vernacular 'booby' refers to the garish facial colours, like clowns (*el bobo*), or alternatively may reflect the stupidity which clowns feign, since boobies seem similarly stupid in that they are easy to approach and kill.

Gannets, like pelicans, have entered written European folklore in a way that does not apply to boobies. Pre-Darwinian accounts of animals were often human-centred and mythological. An interesting example is the myth of the origin of the barnacle goose or, as it may be, the soland goose, for the two were sometimes confused, though not, of course, in the flesh. They were thought to originate from the goose-barnacle, a crustacean which adheres to wood. The origin of the myth lies in the curiously feathery appendages of the goose barnacle, with its beak-like shell and marine habit. 'So rotten sides of broken schippes do change to Barnacles; O Transformation strange. T'was first a greene Tree, then a Gallant Hull, lately a mushroom, now a flying gull' (Turner 1544 quoted in Evans 1903). Turner also wrote 'the chenerotes' (that is, the mythical birds) 'are either Bernicles, or the geese of the Bass' (that is, gannets). Armstrong (1958) cites the *Exeter Riddle Book*:

Low was I besunken; in the sea I waxed; over-
covered with the waves, clinging with my
body to a wandering wood. Quick the life I
had, when I from the clasping came of the bil-
lows, of the beam wood, in my black array;
white in part were then my pranked garments

fair, when the lift upheaved me, me a living creature, wind from wave upblowing; and as wide as far Bore me o'er the bath of seals—say what is my name?

Armstrong then plumps for the little auk as the bird to which the legend refers. In particular, he points out the bird's blackness. In fact it fits the juvenile gannet better. Part of the myth depended on the equinoctial appearances, gale-borne, of ships' timbers riddled with goose barnacles, the very time that barnacle geese also appeared. But it is also the time at which many migrating juvenile gannets are cast ashore. In fact they were taken and eaten off the coast of France, which is passed by thousands of black gannets but where there are no barnacle geese. Moreover, Mouffet's (1665) comment, ostensibly about barnacle geese, fits the juvenile gannet equally well: 'Barnacle taste very unsavoury. Poor men eat them, rich men hate them, wise men reject them when they have other meat'.

With few exceptions, objective observation of animals barely predates early European ethologists. Even though Peter Swave in 1535 correctly noted that gannets incubate their egg beneath their webs, a habit that a few minutes' fairly casual observation could verify, he was widely disbelieved (see Wegener, 1861–65). But the apparently foolish observation that 'these solem geese, when their eggs are sufficiently sitten, they stamp upon them with their feet and break them' could easily be correct and refer to those (few) females that fail to transfer the hatching egg to the top of their webs and thus stand (though they do not stamp!) on their hatchling. The Atlantic gannet was probably the first sulid, perhaps even the first pelecaniform, to enter written tradition in the form of a detailed record of its habits, in the *Scotorum Historiae* of Hector Boece (1527). Yet one wonders what could have led to the belief, recorded there, that 'these foules doo feed their young with the most delicat fish that they can come by. For though they have already preied upon anie one, and have it fast in their beake or talons [sic!], yet if they happen, as they fly toward the land to espie a better, they let the first fall againe into the sea and pursue the later with great and eager swiftnesse until they take hold

thereof'. Could it refer to a kleptoparasitic attack by a great skua?

Gannets were perhaps the first seabirds to be ringed though other seabirds, such as frigatebirds in the Gilbert Islands, had been marked. A correspondent of Harvie-Brown wrote, 'I wonder if you can tell me who is labelling the young gannets at the Bass, for the other day when cruising between North Berwick and Elie I sailed down one of them and found on its leg a bangle with the words "Bass Rock 1904" engraved on it' (Nelson 1978a). (The ringer was probably E.T.Booth who also bred gannets.)

Long before modern devices, gannets were used by fishermen to indicate the whereabouts of fish. Angus Martin (in Nelson 1986: 292) collected some of the Clyde lore from fishermen of Girvan and Kintyre, near to the great gannetry of Ailsa Craig:

... we wir doon along Machrie, an when it cam late evenin, there wir boats ringin and markin two or three machrel. We left an wir crossin for Torrisdale there, an we had the sail on—I think the win wis fae the nor'ard, an I said tae the ould fella, says I: 'look at them gannets aheid o' us there, on the top o' the watter. Thats herrin' says I, 'up on the surface'. The gannets were skitein in laik that ... an its gettin dark. It wad be aboot the month o' June. He says 'we'll try it. Lower the sail'. An thir wis a wil' bit o' grum'lin. We shot, an by God, we got a fine fishin'. Well, we had herrin' every night that week, lookin fur them kinna gannets. Wan!. If we seen wan, thats good enough ... We owe a great lot tae the gannet. I've got a thousan poun' fur a shot on a gannet. A gannet strikin' ... its no an infallible thing ... but if ye see him comin doon straight, nine times oot'a ten he's on herrin', an if ye see him in on the shore head, its mostly in on scaffas an wee cuddains an things lik' that.

'We used to go along watchin' fur the gannets. Ye'd see them comin oot o' the sky. When ye'd see them hingin thon wey, cockin thir neb, that's when the herrin' wir recht thick. Ye used tae try an get the net oot

afore the gannet wid strik'. A rally o' gannets. They gather, just a few, an' they went roon' an roon' till the sky wis white. I think, withoot an untruth, there'd be a thousan gannets in some o' these rallies, an' ye could hear the noise a mile away, them goin' down 'plop', an' an odd time ye saw the unfortunate one that hed been het by some o' the ithers. But how they managed tae steer clear o' wan anither—they must hae had automatic pilots.

Two modern poems close this brief literary account.

*In this moment
while the fish is dying
now the gannet turns and peels over
out of its holding pattern/flips/and capsizes,
and
falls slowly in the foreshortened distance,
as a stone dropped from some monstrous
headland
seems while one leans
to dawdle midway in its plummet.
Wings flutter at first then cease
held back rigid-stiff in the slip-stream punch
and buffet of the kicking air.
Then still falling/still vertical, he is struck,
like a paper dart flung at a fan/struck and
spun like a loosened weathercock yet
vertical still and able
to stabilise again and then
flip and yet fasten again/and again/and still/still
still the plunge goes on now
in this moment/last second
now while the sun strikes
and the swell gathers
and the gannet is closing
and the fish is dying.*

(Anon.)

God's Dominion

*Gannets
before the fall, before
the sixth day, plunged
from brow to base*

*a hundred feet
of the Bass cliffside
with the weight and
speed of a plummet
the slant sea riving.*

*Gannets no doubt
when man is redeemed
or redundant will
nest on the wreckage
of the world he leaves;
spread their wings
to the measure of man
and continue in calm
their immaculate diving.*

(Simon Baynes, personal communication)

Sulids have been and still are exploited for food. Again, the oldest accounts refer to the Atlantic gannet. Prehistoric man must have preyed on gannets at the breeding colony; they are large, nutritious, closely packed and reluctant to flee—a bountiful source of meat. Migrating juveniles, too, might have been catchable. Their bones have been excavated from the epi-palaeolithic level on the Mediterranean coast of Spain (Eastham 1987). Gugas (young gannets) used to be a delicacy at Scottish banquets: 'amongst our viands that we had I must not forget the soland goose, a most delicate fowle which breeds in great abundance in a little rocke called the Basse' (Brereton 1634). Gannetries in Scotland, the Faroes and Iceland were raided for gugas and sometimes adults as well. The huge colony on Bird Rocks, Canada, was almost eliminated by man. St. Kildan sea-fowlers based almost their entire island economy on seabirds, particularly gannets, fulmars, and puffins, whose cleat-dried carcasses sustained them through more than a thousand winters. The uses to which they put gannet parts included shoes and stockings (the everted skin of head and neck with beak removed), lamps (the sternum), skin bottles (stomachs and gullets), pipe-stem (ulna) and purse (webs). At the other end of the world, Maoris partook of the gannet's fabled strength by inserting its white down in their hair and attaching it to their ears. Today they are still taken in the Faroes and the only Scottish gannetry still legally raided for

gugas is *Sula Sgeir* (see Beatty 1992 for a recent and wonderfully illustrated account). The harvest is limited to 2,000 under an agreement with Scottish Natural Heritage. The annual trip is a major event in the life of the isolated community on the Isle of Lewis but it now appears that the men of Noss have developed a trade in gugas beyond the original tradition, which probably contravenes EEC Conservation legislation though I suppose the Commission are more interested in the shape of bananas.

Wonderful were the cures attributed to gannet fat. In *Ein Mittelenglisches Medezin Buch* of the 15th and 16th Centuries, gannet grease is recommended, along with badger and boar fat, as a cure for gout and to Canon Hector Boece of Aberdeen (1527) is attributed the oft-quoted passage: 'within the bowellis of thir geis is ane fatness of singulaire medicine; for it helis mony infirmities speciallie sik as comis be gut [gout] and catar [catarrh] disceding in the hanches or lethies [groins] of men and wemen'. Later, alas, the value of gannet fat descended to that of axle grease, boot grease and sheep-smear. The feathers were worth 10 shillings (50p) for 14 lbs in 1900 and it was reckoned that the feathers from at least 240 gannets were required to stuff one mattress.

Cormorants/shags

Turner (1544: 207) condemns the name 'cormorant' as a corruption:

... for it [the puffin] is not a voracious bird, as our corvorant is, which you (dearest Gesner) rightly name *Corvus aquaticus* ... while our people corruptly say cormorant, not knowing from the derivation of the word that it ought to be called the crow that devours, and this it does naturally, since it is endowed by nature with only one intestine straight and without a coil ... on account of the vehemence of the natural heat, which very quickly consumes all that it swallows.

Cormorant (Latin origin) is anglicized French whilst *Phalacrocorax* (Greek origin) refers to the bare facial skin and means 'bald raven'.

Like gannets, cormorants have been much used as food. A midden in Argentina, from more than 4,000 years before present, has yielded an abundance of imperial shag bones (Rasmussen *et al.* 1994). The double-crested cormorant was harvested at least as early as the 17th Century in New England and Newfoundland. Around the Kuria Murias the Socotra cormorant used to be hunted for food. Morris (1994) records the methods, which compare closely with those used by the fowlers of St. Kilda; daring exploits on high cliffs, using hand-spun ropes. Exploits were enshrined in song and story. The Bat'hari tribe have a strange song which incorporates a resonant mouth music, said to be irresistible to cormorants. Hunting was done at night and it seems that very large numbers were killed. Eskimos used the skin of the pelagic cormorant as clothing and the Chinese exploit cormorants as medicine. Del Hoyo *et al.* (1992) state that in some native populations cormorants and other seabirds comprise up to 10% of the diet, but this culling was succeeded by far worse slaughter as indigenous human populations were supplemented or supplanted by European immigrants, as in Canada and America. The coastal and inshore-nesting habits of cormorants made them easier prey than most sulids. The scale of destruction is shown by the fate of the near-flightless spectacled cormorant endemic to the Commander Islands of the far-western Bering Sea. Little more than 100 years after its discovery in 1741 it was extinct, largely due to slaughter by mainly Russian fur-hunters killing sea-otters and the now-extinct Steller's sea-cow.

In Peru and Chile (and to some extent the Californian Gulf), cormorants, especially, produced colossal amounts of highly nitrogenous guano worth millions as fertilizer. One guanay cormorant yields about 15 kilos of guano per year, more than any other bird species (Hutchinson 1950). Albumen from their eggs makes a useful binder in mortar and was used in Peru and Chile in the 18th and 19th Centuries.

Some cultures, particularly Chinese and Japanese, have for centuries put the cormorant's skill to use (illustrated account in Johnsgard 1993). In Japan birds are caught from the wild and worked in groups from skiffs. The handler lowers them into the water

with a line attached to a neck ring which prevents the bird from swallowing fish. Often, the Japanese fish at night with a lamp in the prow of the boat. After the bird has caught fish, often seven, it is allowed to hunt for itself. The Chinese domesticate their cormorants. The eggs are hatched by hens and the chicks reared on bits of fish, meat and tofu. At the age of natural independence they are wing-clipped and trained to respond to whistles and shouts, presumably by Pavlovian conditioning. The degree of cooperation achieved is astounding, considering the phylogenetic primitiveness of cormorants. Birds will dive at a signal and will jump onto poles to be retrieved. Some boats carry up to 100 cormorants and tow half a dozen rafts, each separately manned and forming a crescent around the parent boat. Each bird returns to its own raft and may disgorge into a container or have its catch removed by hand. Although it sounds like a fisherman's tale, it is said that cormorants will cooperate to hold a fish too large for one bird. In this way fish weighing up to 7 kg can be captured. It is said that a bird which has caught its 'statutory' number of fish will refuse to cooperate further until it has fed. No bird has yet been shown to be able to count up to seven so this feat is perhaps questionable. Trained cormorants are worth \$135–250, which is the equivalent of several months' wages, and they may live for 20 years.

Frigatebirds

Native folklore surrounding frigatebirds is doubtless extensive but oral. Its extreme aerialness is well captured by Whitman: 'Thou born to match the gale (thou art all wings), To cope with heaven and earth and sea, and hurricane, Thou ship of air that never furls't thy sail, through spaces, realms, gyrating' ('To the Man-of-War Bird', 1900). The log of Christopher Columbus, recorded in 'Diario del Descubrimiento' contains the first historical record of the (magnificent) frigatebird, in the Cape Verdes, with a surprisingly accurate description of its habits (Den Hartog 1993).

Tropicbirds

Marchant and Higgins (1990) describe how the name *Phaethon* derives from the association of these

lovely birds with the bright sun of the tropics. *Phaethon*, the shining, was an epithet of *Helios*, the sun, but more commonly the name of a son of *Helios* by *Clymene*. Zeus slew him for driving the chariot of the sun too near the earth. His sisters (*Phaethontides*), who had yoked the horses to the chariot, were metamorphosed into poplars and their tears into amber. The popular English names, which are duplicated in other languages, derive from the long tail streamers or the shrill whistle.

'I hear clear, bugle notes falling like swift slanting rain in a cascading shower. I gaze up and behold a snow-white angelic thing... it is the bright chanticleer of the ocean... fitly styled the boatswain's mate.' (Herman Melville, *Moby Dick*, 1851).

Pelecaniforms and the present

Pelicans

Five of the seven species (great white, Dalmatian, American white, brown and spot-billed) have declined this century. The great white is regionally threatened whilst the Dalmatian and spot-billed are globally endangered. The pink-backed and Australian are still common and/or widespread. Persecution of the American white, brown, Dalmatian and great white still goes on in places but the pink-backed and spot-billed pelicans are often welcomed and befriended by villagers.

The Pelican Research Group (Old World) led by Alain Crivelli is studying pelican biology and collating existing material. The recent publication of Russian research (Crivelli *et al.* 1994), some of it from before the 1939–45 war has pinpointed the world's most important concentrations of Dalmatian pelicans. The need now is for State Reserves and increased protection, particularly for breeding colonies.

The long-lasting effect of contamination by oil is shown in a study of rehabilitated (radio-tagged and colour marked) brown pelicans compared with wild (Anderson *et al.* 1996). The oiled birds showed a higher rate of disappearance (probably dead) and were not recorded at a breeding colony within the next two years.

Pollution leads to eutrophication of some breeding habitats with consequent algal blooms and

death of fish. Although the main food fish of the great and Dalmatian pelicans in Greece contained only low concentrations of pollutants, their levels of DDE exceeded those found in other Mediterranean waterbirds except the great cormorant in the Danube Delta and Cory's shearwater in Majorca (Renzoni *et al.* 1986). The levels of PCBs were low, in contrast to those of the western Mediterranean, which is affected by the greater industrialization of western Europe. Zhatkanbayev (1994a) reports high concentrations of DDT, DDE and hexachlorine cyclohexane in adult and dead young Dalmatian pelicans in the Ili Delta. Analysis of liver tissue revealed significantly higher levels of contamination by several organochlorine compounds in males than in females (Donaldson and Braune 1999) possibly due to females eliminating some toxins via their eggs. But Krivenko *et al.* (1994) suggest that, in future, pelicans will be affected largely by natural factors, mainly changes in rainfall in arid and semi-arid regions of Eurasia.

Like most other pelecaniforms, the range and numbers of pelicans has probably been shrinking for hundreds or in some cases thousands of years but this process accelerated dramatically last century, particularly during the last 50 years. More than half of the breeding sites of Dalmatian and great white in the Palaearctic receive absolutely no protection (Crivelli *et al.* 1991b) and even where pelicans are legally protected they are still killed (in recent years hundreds have been shot in Israel alone and in Turkey at major wintering sites of the Menderes Delta and Lake Bafa, as well as elsewhere, Dalmatian pelicans are still regularly shot, for 'sport'), though in the former USSR significant fines are imposed on those who kill pelicans or steal eggs. On remote islands in Lake Manitoba and Winnipeg, huge numbers of American white pelicans are killed. In 1994 more than 2,000, including young, were killed on Winnipegosis and in 1995 more than 600 on Gull Island in Lake Manitoba. Recently reported atrocities against pelicans in Canada have included the use of flame throwers to incinerate live adults and young (Canadian Society for Endangered Birds).

The situation has deteriorated most markedly in the Dalmatian and spot-billed, both of which now

have dangerously small populations (Sp Acc) and reduced breeding ranges. Within Roman times Dalmatian pelicans bred in estuaries such as the Thames, Scheldt, Rhine and Elbe, and numbered (estimated) millions in eastern European countries such as Romania, from which they are now absent, or nearly so. Even though there may well be some unrecorded colonies in China and Russia, these are unlikely to alter its endangered status. The spot-billed may not have suffered quite such a demise but, nevertheless, it is probably the least numerous pelican, now confined to SE India and Sri Lanka.

The other pelicans present a brighter picture. The great white is still common particularly in Africa and parts of Russia, but is regionally threatened, most seriously in parts of the western Palaearctic where once it was abundant. Its replacement species in North America, though decidedly less numerous, is thought to be stable or even increasing after a decline in the 1940s to 1960s, but breeding birds are still killed (see above). The Australian pelican remains stable and common. The arboreal pink-backed is less vulnerable than the ground-nesters. It is notably tolerant of man and because its colonies are small, it is less dependent on locally superabundant food. Its wide African distribution prevents any realistic estimate of overall numbers, but it is common. The brown, now most numerous, has suffered heavy regional losses giving rise to local concern, but has partly recovered.

The main causes of the decline in pelicans are loss of feeding and breeding habitat through the drainage and reclamation of wetlands, or other forms of water-level management such as dam building, for agriculture or building; industrial, agricultural, and domestic pollution of waterways and other man-related causes of death and breeding failure. Only 5% of breeding grounds are legally protected and this is often ineffective despite theoretical safeguard in EEC countries of the Bonn and Bern Conventions. The extent of these problems is evident from the Species Accounts and the following extract (Zhatkanbaev 1994b):

... at the present time the Ili River delta is a varied complex of landscapes consisting mainly of an extensive network of river

channels . . . a series of lakes with running and standing water, extensive reed-beds and typical desert biotopes on islands between river channels . . . Regulation of the Ili River flow by the Kapchagai hydroelectric station, and the creation of the irrigated agriculture downstream of the reservoir resulted in intensive drying-out and a decrease in the delta area. The hydrological regime of the delta's river channels and the dynamics of riverbed processes were changed. Major summer flooding ceased almost completely, the level of the water table fell by 1–2 metres and soil drying out and salinisation became evident . . . Widespread mowing of grass and reed and constant fires in reedbeds and riverine scrub are other important factors . . . The hydrological regime of the delta is now very unstable especially in the winter and spring/summer period—the time when most water-birds are nesting.

He recommends the establishment of a reserve of c. 65 000 ha in the Delta with sensitive control of water levels to ensure appropriate nesting areas.

He is writing about probably the most important area in the world for the Dalmatian pelican and for non-African populations of the great white. Perhaps the main hope for them is environmental education and locally enforceable protection, possibly with compensation. Unfortunately, wetland drainage, agriculture, and industry are political issues which are not amenable to the measures which bird conservationists would espouse. The expanding European Community which in theory offers protective legislation simultaneously funds developments which hugely undermine conservation. In the more eastern countries, whose membership is anticipated, this will pose serious problems for pelicans and other wetland birds.

Where populations are local, small and vulnerable, as in the Dalmatian and great white in Greece, practical measures such as the provision of floating nesting platforms and dredge spoil islands (e.g. Pyrovetsi 1997) with models and play-back of vocalizations, screening, the prevention of disturbance, and the flagging of overhead powerlines

(many die in collision with these) are not to be despised, but the preservation of adequate breeding and feeding habitat remains paramount. Due to increased extraction of water some lakes and rivers have dried up completely in recent years, including Lake Oubeira in Algeria, Lake Marmara in Turkey, and the Axios, Nestos and Strymon rivers in Greece.

Grummt (1983) and Brouwer *et al.* (1994) provide valuable information on the management and breeding of captive pelicans, which may prove a useful conservation tool, although hatching and breeding success is extremely low. There are, as yet, no self-sustaining populations of captive pelicans, but between 1930 and 1982 all species except the Australian bred in zoos (Brouwer *et al.* 1994) and since 1991 the Poznan Zoo (Poland) has bred great white pelicans (Smielowski 1995). The Khao Khieo Zoo (Thailand) has a breeding colony (nearly 200 birds) of spot-billed pelicans (Saenger and Helfert 1996). Ober and Verhade (1998) describe artificial incubation and hand-rearing of great white pelicans. Between 1961 and 1983, 24 pelicans were hatched at Tierpark, Berlin, (18 great whites, two American whites, two Dalmatians, two brown) and improved techniques, for example regularly providing live fish, could produce better results. A group of at least 20 birds is needed for social stimulation and breeding synchronization. As for several pelecaniforms in the wild, so in captivity, unpaired males can interfere with nesting birds and may have to be removed (on captive breeding see Grummt 1983, 1984).

Gannets/boobies

The only rare sulid is the endemic Abbott's booby. Its remaining nesting habitat is now protected and there seems no reason why the population should not be viable. The blue-footed booby probably has declined but is still numerous within its comparatively restricted distribution. The Peruvian, though even more restricted, has until relatively recently been perhaps the most numerous of all, but the collapse of the Peruvian fish stocks combined with recent ENSO has greatly reduced its numbers, though it is now recovering.

The three gannets tell a different story. After severe exploitation, the Atlantic gannet, protected now for over a century, is still increasing especially in the eastern Atlantic, initiating new colonies and adding to old ones, though one cannot say how its present numbers compare to prehistoric ones. Its success, despite the decline of many of its food fish, is underpinned by a wide prey-spectrum, exclusive feeding niche, and perhaps by discards from fishing fleets. The Australasian gannet, too, is increasing and spreading after the cessation of persecution. The African gannet is increasing less than the other two, if at all (Sp Acc), but seems unthreatened although it is not initiating new colonies.

By contrast, the three tropical boobies—brown, masked and red-footed—are in continuing and severe decline in many parts of their still extensive ranges and some previously substantial colonies have been eliminated. Even ‘protected’ colonies are plundered, as in the Caribbean and on innumerable Pacific Ocean islands. The control of pest-predators (rat, cat, dog, pig, mongoose, monkey) is needed on some islands. Large populations have been eliminated or prevented from breeding, for instance masked boobies by cats on Ascension and pigs on Clipperton. Stager’s (1964) elimination of the pigs led to a rapid and huge influx of boobies, from *c.* 150 scattered pairs to more than 4,000. The total pest clearance which is needed worldwide is difficult, enormously costly, and long-term, and has little or no chance of wide implementation within the foreseeable future.

On many hundreds of little visited islands, atolls and cays in the SW and central Pacific, Indonesia, Malaysia, the Indian Ocean, the China Sea, the Caribbean, and elsewhere, destructive pressures are rising. Sea passages are easier using powerful out-board motors and thus native pressures have increased; expanding tourism takes more people to out-of-the-way places; far-ranging fishing vessels, principally Japanese and Indonesian, land on isolated cays and atolls, for example off Australia’s Great Barrier Reef, and disturb and destroy nesting seabirds; destruction of nesting habitat continues, as also does the spread and multiplication of introduced predators. Examples of these phenomena abound but are well-enough recognized not to

need elaboration. Increasing standards of affluence do not automatically reduce persecution of seabirds in tropical areas and may worsen it. Thousands of red-footed and brown boobies were taken on Christmas Island (IO) at a time when living standards were exceptionally high for the hunters. The attraction for them may be enhanced by the very loss of identity which intrusive western culture has entailed.

Abbott’s booby is an encouraging example of effective conservation. Between 1970–71 and the 1980s, about a third of its nesting habitat was felled for mining, and its small population lost possibly 5–10% of breeding adults. The Australian government, guided by ANPWS, in February 1980 declared the SW corner of Christmas Island (*c.* 12% total area with *c.* 20% known nest-sites) a National Park. In 1987 this was extended to cover *c.* 70% of remaining forest and all areas containing nesting Abbott’s. Further clearing was prohibited by declaration of the Australian Prime Minister, and the forest outside the National Park was protected (*National Parks and Wildlife Conservation Act*). Also, 1975–1985, single-handedly and with voluntary funding from the mining company, the conservator (D. Powell) grew thousands of seedlings of trees most used by Abbott’s, for rehabilitating mined-out Abbott’s areas. Mining holes were back-filled with crushed limestone prior to planting. This area has since been extended by the (now) Australian Nature Conservation Agency but it will be several decades before forest usable by Abbott’s will be established (see also Shepherd 1994). In 1989 The Christmas Island Rainforest Rehabilitation Programme aimed at revegetating clearings adjacent to Abbott’s nesting habitat in an attempt, via wind breaks, to reduce turbulence and bird-groundings (Carew-Reid 1987). By creating thermals, clearings encourage soaring frigatebirds, thus increasing the likelihood of kleptoparasitic attacks and consequent grounding of incoming boobies. Fragmentation of habitat favours the endemic hawk and thus the new phenomenon of attacks on small, unattended boobies. For a species on the knife-edge of population stability these minor losses are significant. Proposals in the Australian press to use part of Christmas Island for a space programme causes concern. Hugh Yorkston has recently compiled a detailed proposal nominating Christmas Island and

4.1 Causes of mortality in the Atlantic gannet. (From Nelson 2001.)

<i>Cause of death</i>	<i>Adults</i>	<i>Late immature</i>	<i>Juveniles/Early immature</i>	<i>Total</i>
Found dead, exhausted or injured	156 (38)	47	172	375
Killed by man (almost all by fishermen, deliberately or accidentally in nets, on hooks, etc.)	15 (4)	9	39	118
Oiled	40 (8)	13	15	68
Cause difficult to interpret; includes 'caught', presumably by fishermen	3 (1)	4	21	28
Killed by discards (line, netting etc.)	5	2	11	18
<i>Grand total</i>				587

Notes: 1. Numbers in parens are recoveries from birds ringed as adults; all others ringed as chicks on Bass Rock.

2. Recently, Camphuysen (2001) has analysed the records of gannets found dead in Holland between 1970 and 2000. Most were oiled or entangled in fishing gear. 79% of beached adults or immatures and 47% of juveniles were oiled, though this has declined over time. Entanglement in fish nets, ropes and, increasingly, nylon fish lines rose significantly from 5% (1977–89) to 7.5% (1990s). Around 450 gannets washed ashore each year.

its territorial waters as a World Heritage Site. Abbott's booby is in IUCN's Red Data Book and Nationally Endangered, Schedule 1 ESPA 1992.

Gross contamination with pesticides affected the Canadian population of the Atlantic gannet in the 1960s. The eastern Atlantic one was less contaminated. Between 1971 and 1986 gannet eggs in Canada and Europe have shown between a three fold to tenfold decrease in the levels of PCBs, dieldrin and DDE (Newton *et al.* 1990). Gannet feathers contain variable amounts of mercury. Walsh and Furness (1987) analysed feathers from several colonies. Bass Rock adults had high levels but chicks had low, suggesting that the adults may winter in contaminated areas such as the North Sea, though it is possible that the mercury may come from metal-rich upwellings. Toll due to toxic chemicals cannot be estimated because death may occur only when birds are stressed and mobilization of fat releases dangerous concentrations. It is impossible to disentangle natural from induced mortality; some gannets contain high levels of toxins.

Synthetic waste is a hazard; 97% of nests in a Canadian colony contained plastic, 78% from fishing nets and lines, and the remainder assorted rubbish (Montevecchi 1991). Plastics kill substantial numbers of Atlantic gannets (cordage found in up to 75%

of nests, gannetries differ in the proportion of fouled nests; see Norman *et al.* 1995 for Australasian gannet).

Oiling may seem unimportant to gannets: 35 recovered from a kill estimated at 15,000–30,000 seabirds, mainly auks; 45 compared with 7,757 auks recorded from estimated kill of 50,000. Whilst these figures do not represent the actual number killed, they indicate the relatively low mortality due to oil. However, the percentage of oiled carcasses is higher than for cormorants and shags; of 196 recovered in the National Beached Bird Survey (1991–95), 32.6% of gannets were oiled compared with 8.8% of 1,749 cormorant-shag recoveries. In the Netherlands, though Beach Survey recoveries were few, 75% were oiled (Camphuysen 1993). Juveniles are more at risk than adults because, at first, they are well inshore and swimming rather than flying. Of 582 deaths of Bass-ringed birds, 11.7% were due to oiling.

Man kills huge numbers of the pan-tropical boobies, wiping out entire island populations such as the brown boobies of Pulau Perak and persecuting breeding populations of red-footed and masked boobies throughout vast areas of the Pacific and on some Caribbean islands. Fishermen (European and African) kill, accidentally or deliberately, numbers

of Atlantic and African gannets, both adult and young, for example juvenile African off Angola and French Equatorial Africa. A large proportion of Bass-ringed birds (Figure 4.1) die through entanglement and deliberate killing. The old line-fishing with her-ring- baited hooks illustrates their vulnerability—one haul brought *c.* 200 dead gannets on board. Although insignificant in demographic terms, the barbaric behaviour of some fishermen in tying a gannet's head to its foot, or tying two gannets together by the head and releasing them to die painfully, is a reminder of some men's attitude to wildlife.

On 25 May 1988 *c.* 50–100 inexplicably dead and dying gannets were seen 1 km NE of the Bass; several appeared to have twisted or broken wings (F. Marr personal communication); an underwater explosion may have affected a raft of gannets.

Cormorants/shags

These fall into four groups: common and wide-spread; abundant but with limited distribution; wide-spread but not abundant and in some cases declining; and endemic with small or very small populations. Around 11% of species are at risk (Duffy 1995), largely the tiny populations of vulnerable endemics. The family contains many rare or comparatively rare species: king, Stewart, Chatham, Auckland, Campbell, Bounty, Pitt, Heard (down to 300–800 birds and still killed by man), Crozet, Kerguelen, and Macquarie shags and flightless cormorant; some of the rarest seabirds in the world. Species which have declined this century, in a few cases to near-threatened levels, include Cape, Socotra, bank, Japanese, guanay, red-legged, little pied, crowned, Javanese, pygmy, and black-faced cormorants, and South Georgian and spotted shags. Most are naturally restricted populations and merely need protection. Only one cormorant, the endemic spectacled cormorant of the Bering Sea Commander Islands has become extinct within recent times (around 1850). Species which are neither rare nor endemic or, if they have declined, are now increasing again, at least in some regions, include great, double-crested, neotropic, little black, great, Indian, Brandt's,

pelagic, red-faced, pied, and long-tailed cormorants, and European, rock, imperial, and Antarctic shags. The anhinga and darter also fall into this category.

Many of the sub-Antarctic cormorants numbering fewer than 1,000 birds occur only on one island, or island group, such as the Chathams, Pitt, Heard, etc. The rarest may be the king shag, with fewer than 300 birds. Loss of adults is particularly serious and when fishermen kill even a few of the endemic island shags they endanger the species. The drainage of wetlands has been hugely detrimental; the pygmy cormorant, for example, is now threatened. Some species with large, continental populations, as in Europe and North America, have lost feeding and breeding habitat. Conversely, man-made reservoirs, irrigation systems and fish farms have benefited some species such as the neotropic cormorant in South America, the double-crested in North America and the little black in Australia.

Like other pelecaniforms, cormorants absorb pollutants such as heavy metals, selenium, PCBs and DDT derivatives (DDE causes eggshell thinning), and some of these accumulate with age (Sepalveda *et al.* 1998). Van-Eerden and Schoonbee (1996) showed that long-tailed cormorants accumulated abnormally high concentrations of cadmium, copper, nickel and lead. By a process called 'biomagnification' pollutants in cormorants reach concentrations higher than those found in their prey (Falandysz *et al.* 1997). After 1945 organo-chlorine pesticides, widely used in the Great Lakes Basin of North America among many other places, led to drastic thinning of eggshells in the double-crested cormorant which, by 1959, on Lake Superior, were 27% thinner than normal. By the 1970s the cormorants of this region were the most heavily contaminated phalacrocoracids in North America and possibly the world, and breeding success was practically zero despite this cormorant's spectacular recovery, in some areas doubling or tripling its numbers every few years. Double-crested cormorants from the Canadian Great Lakes were contaminated with organochlorines which were linked to chicks with bill deformities in 16 colonies—a fifth of all those surveyed

(Ryckman *et al.* 1998). In the same species in Lake Michigan, PCBs and DDE were linked to the failure of 32% of 1,570 eggs to hatch and with deformed embryos (Custer *et al.* 1999). In the Danube, the eggs of great and pygmy cormorants had more organochlorines than those of most other aquatic birds (Aurigi *et al.* 2000). Cormorants breeding near the contaminated Rhine and Meuse had severely reduced breeding success compared with several other Dutch colonies (Dirkson *et al.* 1995a), mainly because of egg loss. Even in areas where organo-chlorines are no longer used, their residues remain at levels (about 5 parts per million, fresh weight) high enough to accumulate within the bodies and eggs of cormorants and pelicans. On the other hand, Pyle *et al.* (1999) concluded that organo-chlorine contamination in Brandt's cormorant (Farallons) does not currently pose a problem.

Cormorants are far more likely than sulids to suffer from inshore oil contamination. As surface divers, swimming far underwater, they are more likely to emerge into an oil slick. The Exxon Valdez disaster in Alaska caused an estimated 100,000–300,000 seabird deaths, including many pelagic cormorants, whilst oil pollution in the Persian Gulf killed many Socotra cormorants. The wreck of the Braer in 1993 killed about half the local population of European shags.

Organized slaughter by fishermen is far from unknown. In Canada (1994, Lake Winnipeg) 4,000–6,000 double-crested cormorants were killed by shooting, burning with flame throwers and trampling young, and more than 1,000 on Gull Island, Lake Manitoba, in 1995 (Report of Canadian Society for Endangered Birds). Great and double-crested cormorants are killed in large numbers by fishermen and aquaculturalists because of their damage to commercial stocks of salmon, trout, and catfish. From 1987–94, 5,335 great cormorants were shot in Poland alone—nearly a fifth of the total mortality. In southern Norway some 20,000 were killed each year (Barrett and Vader 1984). Others deliberately killed include black-faced, pelagic and neotropic cormorants, king, spotted and European shags and several endemics.

But depredations on fish may be overestimated. For example, the great cormorant eats large quantities of non-commercial species, some of which, in the wild, prey heavily on salmon smolts. Nevertheless, many European countries such as Italy, Poland and the Czech Republic, consider cormorants highly detrimental to fishery interests. The classic case of conflict between cormorants and commercial fishing interests is that of the double-crested cormorant in the Mississippi delta (see Nettleship and Duffy 1992 for a thorough evaluation). Catfish aquaculturists have invested large sums in fish farms and, traditionally, have seen the solution of the cormorant problem as wholesale destruction of the birds. Because of considerable damage which the nesting cormorants were inflicting on a riverine ecosystem in the St. Lawrence, a reduction was sought there, too. The results are of considerable interest. The St. Lawrence river population had grown from around 6,000 breeding pairs in 1979 to nearly 18,000 in 1989 and a projected 27,000 pairs by 1993. Modelling suggested that the population could be reduced to around 10,000 pairs by simultaneously lowering recruitment (by spraying the eggs with oil in three-quarters of all the nests in ground colonies) and shooting about 2,000 adults. By 1991, after three years of culling, the estuarine population had fallen to 12,000 pairs even before the effects of spraying could have been felt. Whether there had been emigration remained unproven. It is now considered that the effects on the cormorants have been more drastic than was envisaged. Non-killing options include: removing favoured nesting or roosting trees within range of the fishery; multiple forms of harassment; stocking fish at lower densities to make it more difficult for birds to spot them from the air; modifying management practice by, for example, segregating age classes and protecting those ponds with the most valuable classes; stocking with fish after the cormorant's main migration period, when thousands use the Mississippi flyway; stocking when cormorants require least food; restricting runways for take-off; steepening pond sides; increasing the turbidity of the water; diluting commercial prey with non-commercial species and crustacea. However,

psychology is involved. A dead cormorant cannot eat fish so, despite the ambiguity of the evidence linking, for example, cormorant predation of salmon smolts with the number of adult salmon which return, the demand for cormorant culls intensifies. In Britain, readers of angling magazines dumped hundreds of rotting cormorant heads on the doorsteps of conservation agencies.

Accidental mortality mainly attends entanglement in nets and pots or on hooks. Engstrom (1998) found a maximum of 0.24 cormorants drowned per fyke net per day. Fiske and Rov (1997) found that the main cause of death in the great cormorant was drowning in fishing gear (62.3%) against 19.4% shot.

Finally, many cormorants are sensitive to disturbance and colonies may be entirely deserted as a consequence.

Large broods and short periods of deferred breeding endow some cormorant species with spectacular productivity. This increases their ability to recover from catastrophic reductions, whether natural, such as ENSO, or man-induced, but large, local populations open them to persecution. Indeed, far from cormorants having affected man, his over-fishing may have affected the Cape cormorant off South Africa, despite which, there have been serious attempts by the fishing lobby to destroy birds. The commercial value of the guanay cormorant of Peru has saved it from resentful fishery interests but other species lack this special value.

Guano on arid islands is valuable but can cause undesirable eutrophication of lakes. In 1983, at Lake Balaton in Hungary, 1,500 pairs of cormorants and their young took up 12.5 tons of nitrogen and 3.1 of phosphorus, of which all but c. 2% was excreted, mostly, presumably, into the lake (Geza and Sandor 1992).

Man-induced mortality is slight compared with natural oceanic phenomena which affect food. But, on past experience, food failures such as may occur in the Humboldt, Benguela or Californian currents, and which kill millions of seabirds, including cormorants, would be followed by rapid recovery were it not for the additional factor of overfishing by man. It is this double impact which has delayed the recovery of the Peruvian guano birds, especially

the guanay cormorant, which was the most numerous of them.

Anhinga/darter

The widespread breeding distribution of the old-world darter and the generally small size and difficult access of its colonies mean that it is not under threat. The anhinga, though less numerous and widespread, is also not endangered.

Frigatebirds

(See, especially, Nettleship *et al.* 1994.) Many populations of great and lesser frigatebirds are in decline or have been exterminated. In parts of the Pacific and Indian Ocean they are still killed for food. As recently as the 1980s, Cocos Malays (Cocos Keeling) were killing hundreds of great frigatebirds, including breeding adults, on the North Island of the atoll. Again, the combination of money, outboards and guns, rather than the need for food, led to the slaughter. This activity is now illegal under Australian law. Considerable numbers of breeding adults of the extremely rare and endemic Christmas frigatebird were regularly taken at least into the 1970s (Nelson 1976). On Aldabra, great and lesser frigatebirds were killed by the thousand by Seychellois in the 20th Century. Magnificent frigatebirds are still taken from Caribbean islands. In the SW Pacific, recent voyages by Angela Kepler (personal communication) revealed widespread killing of seabirds on little-known islands such as the SW Palau group. Frigatebirds and boobies were among the victims. In such an exceptionally long-lived seabird, with a uniquely low reproductive rate, the killing of adults is a drastic drain on the population, though the inevitable decline is slow to be noticed. It is certain that all frigatebird species, with the possible exception of the Ascension, declined markedly in the 20th Century.

In addition to direct human persecution, some populations have suffered from loss of breeding habitat and disturbance, to which they are extremely vulnerable. Natural phenomena such as cyclones and fluctuations in food are not the problem; frigatebirds have survived these since long before man became a menace.

Unfortunately, the very demographic factors which result from the frigatebird's adaptations to its natural hazards, namely long life, low productivity, non-breeding years and long-deferred breeding, together with the widely scattered distribution of the common species, make it extremely difficult to estimate world population trends. A serious decline could be masked for a long time.

Even so, most frigates are far from endangered, although absence of effective protection over most of their range is cause for grave concern. The magnificent frigatebird may be somewhat less affected than the great and lesser because its main areas of population are not among the Polynesian, Melanesian, Micronesian, and Malaysian islands where seabird killing is rife. However, it is still persecuted in some areas, as in the Cape Verde Islands and the Caribbean, and may be much less common in the latter than generally assumed (Van Halewyn and Norton 1984).

Of the two most numerous, widespread and often sympatric species, the great and lesser frigatebirds, the latter is the least abundant, possibly numbering several hundreds of thousands against, possibly, around a million great frigatebirds, though these figures may well be highly optimistic. Little is known about their numbers and distribution throughout the vast Indo-Pacific area, with thousands of islands, but it seems that almost everywhere visitors from a neighbouring island, or from a fishing boat, yacht, naval boat or one of the increasingly adventurous cruise ships are likely to land at some point in the breeding season. A single intrusive visit at a sensitive time can cause great damage or total failure, especially to colonial pelecaniforms and to none more than frigatebirds. Experience in the Galapagos, a famous honeypot, has shown that appropriate controls using guides can be effective, but in most of the frigatebird's far-flung haunts there is no effective protection.

One cannot exclude a detrimental effect of the huge tuna-fishing operations on the surface-feeding frigatebird, partly dependent on large predatory fish driving prey to the surface. The tuna population has already been greatly reduced.

After the great and lesser frigates, the next most populous, the magnificent, may be optimistically

guessed at >200,000 birds. The Cape Verde Island population, now almost extinct, has been pillaged by fishermen and in the Caribbean this species has declined steadily for perhaps hundreds of years. Disturbance, destruction of habitat and direct persecution still continue. The Mexican population may be the world's largest though numbers in South America are inadequately known.

The two endemics are the most vulnerable, especially the Christmas frigatebird, which lost much of its prime nesting areas on the shore terraces. Many mature birds have been killed by Asian workers between the early 1900s and the late 1960s for food; or died by accident in slurry ponds or when attempting to take bait from hooks. There remain only about 1,600 pairs, which is even fewer than the rare Abbott's booby (Stokes 1988). The island is now wardened (Australian National Park) and the destructive aspects of mining have ceased.

The Ascension frigatebird (<10,000 according to Ashmole *et al.* 1994) is restricted to Bosun Bird island following the settlement of humans on Ascension in 1815. Some birds still roost there and some are still killed by cats, though there are plans to eradicate them. Even on remote Bosun Bird there has recently been increased disturbance and until 1977 visitors could land at will. Now it is a bird sanctuary and tourists and photographers are more strictly controlled. Planes do land on Ascension and pose another threat since 'strikes' generate intense pressure for culls.

Cocos Malays killed a large number (probably thousands) of adult and young great frigatebirds. Formerly great numbers of Caribbean magnificent frigatebirds were killed for oil (Palmer 1962), and adults and young are still taken for food and even bait. Over huge areas of the Pacific and Indian Oceans frigatebirds are few or absent due to human persecution dating back hundreds or thousands of years.

Tropicbirds

These have traditionally been killed for their plumage and magnificent streamers, widely coveted in Polynesia and Melanesia, and collection of adults, young, and eggs continues over much of their

range. Until comparatively recently the red-tailed tropicbirds on Christmas Island (PO) were heavily exploited and the population hugely reduced, but since 1977 protection has helped it to recover slightly. In parts of the SW Pacific, for example Cook Island, large numbers of red-tailed tropicbirds are still killed on specially organized trips (Kepler personal communication); she notes the complete lack of enforcement of protection even where legislation exists. Tropicbirds have suffered, also, from the usual introduced predators, particularly Polynesian and black rats, but also cats, dogs, mongooses, racoons, monkeys (*Cercopithecus* spp and rhesus macaques). The latter exterminated at least five species and a probable total of *c.* 10,000 pairs of seabirds from Desecheo Island (Greater Antilles), after their introduction in 1966. Apart from direct predators, rabbits and goats affect some seabirds by destroying vegetation. Intensive use of poisoned rat bait brought increased breeding success of the white-tailed tropicbird (*Culebra National Wildlife Refuge, Puerto Rico, Schaffner 1991*). The more powerful red-tailed may be less susceptible, though ground nesters are predated and on Kure rats were the main cause of loss in all years (Woodward 1972). Although none of the three species is globally threatened, all declined considerably in the 20th century.

In sum, and excluding the endemics, almost a third of the pelecaniforms are either stable, increasing or recovering from former decline; two-thirds are declining. But 45 species (70% of the Order) are still relatively abundant. The comments of Van Halewyn and Norton (1984), with respect to Caribbean seabirds, apply forcibly to some other regions and, so far as breeding colonies are concerned, are well worth repeating: 'We regard widespread and often large-scale collecting of eggs and, to a lesser extent, chicks as the major seabird conservation problem in the region. We hold it responsible for marked declines in the size of breeding populations of most species. Chicks of at least some of the larger species are collected (e.g. frigatebirds, boobies and brown pelican). Adult birds are shot, snared, netted or caught on hooks and by hand at nesting sites, roosts and in coastal waters (e.g. black-capped petrel, frigatebird, boobies and terns). Eggs, chicks and adult birds are still collected for human consumption' and (they detail) for other purposes. When one considers that many of these casualties are breeding adults of long-lived seabirds with low or extremely low productivity, the depredations are cause for deepest concern. Added to pressures mentioned elsewhere, they show why seabird populations are in such serious decline.

General family accounts

Pelicans

Introduction

The seven pelican species are closely related and, with cormorants, anhingids, and sulids form the core of the Order. They are largely freshwater birds whose breeding biology is dominated by the need to catch large quantities of fish comparatively near to the breeding colony, a requirement imposed by the enormous biomass of the brood and its rapid growth. If the colony itself is huge, the demands on local food sources are enormous. Moreover (apart from the brown pelican), having largely forfeited the sea and specialized in fishing in shallow water, from the surface, their colonies are highly dependent on productive lakes and wetlands. Nevertheless, they have achieved a wide distribution and, until recently, their world populations were large or extremely large. Now, unfortunately, most species are threatened or even endangered.

Pelicans will breed in captivity, and this has provided valuable information on behaviour and ecology.

Classification

Of the seven species, adequately covered by the single genus *Pelecanus*, the great white, American white and Australian may be 'replacement' species, taking over from each other in different regions. The Dalmatian is closely related to them and often forms intimately mixed colonies with the great white. All are big, nesting in large groups on the ground or in low vegetation. The spot-billed and pink-backed are smaller and nest in trees, whilst the

brown pelican, distinctive in its plunge-diving and marine habit, nests both in trees and on the ground.

The bird

Voice

Away from the colony pelicans are usually silent though they may be noisy during cooperative feeding. The large young produce a weird assemblage of sounds audible from afar—whines, screams, and yelps, higher-pitched than adult calls. Adult pelicans are mainly restricted to grunts, croaks, hisses and rattles. The syrinx is apparently unmodified; it has no special structures and no flexible tympanic membranes to produce many different sounds. The great white 'moos', possibly by some form of resonance within the pouch. Some pelicans bill-clap loudly with head thrown back; together with frigatebirds, the only pelecaniforms to do so.

External features and anatomy

Pelicans are typically mainly white with extensive black on the wing-tips; melanin presumably strengthens the feathers which are subjected to considerable pressure in soaring flight. Some species are tinged yellow or pink due to carotenoids in the diet and contained in the preen-oil. The yellow-orange may be acquired from colloidal suspensions of iron compounds. These colours are not confined solely to those areas accessible to the bill or the head-rolling by which birds transfer the secretion from the preen-gland. The iridescent greens and blues of cormorants and frigatebirds are entirely absent.

Like several boobies, cormorants and the white-tailed tropicbird, the brown pelican has evolved several plumage types but unlike them no single breeding population of pelicans contains more than one morph. Isolated populations have formed subspecies, as in the Galapagos and Peru.

Pelican chicks, at first pink and naked, grow their first generation of white, grey, brown, or black woolly down in the first week or so. Second-generation down is usually darker but, as in the great white, may be paler. Adult contour feathers do not grow from the same follicles as this down and lack aftershafts. Juveniles are brownish, mottled fawn or distinctly off-white at least on the upperparts, with drab heads and bills. Although by the end of the first year they resemble adults in body plumage, it may take three or four years to acquire full colours. Like juvenile cormorants and boobies, young pelicans tend to show obvious thigh patches and marked pectoral bands or demarcations on the upper breast. These, and the marked occipital crests or outgrowths, may be ancestral traits.

Pelicans generally show bare lores which, together with other bare facial skin and the gape, may surpass even the boobies in extravagant colour—yellow, pink, orange, and mauve. The bright reds may be due to superficial capillary networks. The occipital crest is conspicuous in breeding birds, as in many cormorants (perhaps oddly, no sulids develop a crest although Abbott's can keep its forehead feathers flat whilst raising the feathers of the crown). In the pre-laying period some pelican species develop brightly coloured outgrowths on the forehead or bill but these, together with the nuptial colours, are lost or reduced once the eggs have been laid.

The pelican bill is hugely elongated as a proportion of the length of head and body. As in cormorants there are two grooves on the upper surface, running from the rudimentary external nostrils to the nail on the bill tip. Apparently, however, the secretion from the salt gland does not flow down this groove but passes from the internal nares (the externals being closed) onto the roof of the mouth and thence to the bill tip (brown pelican). As in sulids, pelicans with the bill closed breathe by means of a plated gap at the angle of the gape. The mandibles are smooth-edged, tipped with a prominent nail.

Pelicans seem able to detect fish in muddy water, apparently via the sensitive bill-tip.

The quintessential pelican feature is the hugely distensible gular pouch which, partly due to the flexible rami of the lower mandible, bent by the powerful tongue muscles, can be greatly stretched. The movable upper mandible increases the extent of the gape. The occipital condyle (a bone of the skull) which in cormorants is somewhat flexibly attached to the occipital crest, and to which are attached the muscles which close the mandibles, is absent in pelicans (see Johnsgard 1993 for details of the skeleton). Presumably their feeding method reduces the importance of a firm grasp on prey.

Pelican tail feathers (20–4) are short, giving a squarish tail rounded at the corners beyond which the feet may partly protrude in flight. Wings are notably long (forearm longer than upper) and broad, with rounded tips. They contain 11 primaries (outermost tiny) and an unusually large number (30–35) of secondaries which give the wing its length. The brown pelican (wing area 0.450 m^2) has a wing aspect-ratio of 9.80. Excluding the minute 11th, the longest primary is the second or third outermost. Emarginations produce a markedly fingered wing. Large wings reduce relative wing-loading and facilitate the soaring flight important for the long foraging trips of breeding pelicans. Hartman (1961) calculated a mean wing-loading of 0.84 g per cm^2 for the brown pelican, which is significantly less than most cormorants. The pelican's buoyancy index (a measure of 'lift') was 4.22 compared with 3.27 for the neotropical cormorant and 5.28 for the magnificent frigatebird. This indicates that the pelican attains some 80% of the theoretical soaring ability of frigatebirds even though the latter are supremely adapted for soaring. The sternum is comparatively broad with a fairly shallow keel which, as in frigatebirds, is completely fused with the furcula thus making the pectoral girdle more rigid, which again facilitates soaring. The flight muscles are comparatively small, comprising in the brown pelican some 13.2% of total body weight. Nevertheless this is more than in neotropical (12.7%) and double-crested cormorants (12.6%). The prolonged horizontal position of the wings in gliding flight is facilitated by a deep layer of slow fibres in



5.1 Brown pelican in flight.

the pectoralis muscle (Meyers and Mathias 1997). Despite their large wings and light bones, most pelicans are so heavy that they experience difficulty in becoming airborne unless assisted by wind. Particularly in the tropics they depend to a large extent on thermals to gain height. Worcester (1996) suggests that the relatively flexible feathers of large birds such as pelicans reduce stress on the wing bones during take-off and landing. In flap-glide flight brown pelicans attain a mean speed of 34.3 km per hour and in gliding flight 41 km per hour. Greater speed when gliding than when flapping or flap-gliding is the reverse of the case for frigatebirds (data in Penny-cuick 1983b). The major pectoralis muscle in the American white pelican, and presumably also in others, contains 'fast twitch' fibres in the superficial layer but slow fibres in the deep belly (Rosser *et al.* 1994). They suggest that the superficial fibres serve flapping and the slow fibres are used in soaring flight.

The great white and Dalmatian pelicans are the heaviest flying seabirds in the world; at a maximum *c.* 15,000 g some 4,500 g heavier than the ones with the largest wingspan—the royal (*Diomedea epomophora*) and wandering (*D. exulans*) albatrosses. Bulk is an essential adjunct of pelican fishing technique which entails wielding a pouch which may hold 13,000 g of water, plus fish. Upon this capability rests much of its breeding biology. The smallest pelican, the *occidentalis* race of the brown—the only plunge-diving species—may weigh little over

2,000 g; considerably less than some cormorants and the Atlantic gannet. Between, in descending order, are Australian, American white, pink-backed and spot-billed. However, there is enormous variation in some species, the heaviest recorded weighing three times as much as the lightest which may correlate with different feeding niches. Possibly, the youngest chicks in species which rear more than one fledge at considerably below normal weight and become small adults. Male pelicans are larger than females whereas in boobies, some cormorants, and the frigatebirds the reverse is true.

The pelican's pelvic girdle is broader and shorter than that of cormorants. The synsacrum is only twice as long as broad, whereas in cormorants it is three times. Compared with cormorants the pelican's pelvic proportions and comparatively small leg muscles indicate that they are less powerful swimmers, which is evident from their feeding methods. In pelicans, again as in frigatebirds, the bones of the appendicular skeleton are less dense than in cormorants. In the American white pelican the skeleton averaged about 7% of body weight compared with about 6% for the magnificent frigatebird. But the figures for cormorants are similar to those for pelicans, which may be due to the proportionately greater-sized bones of pelicans. Even the nearly non-pneumatic skeleton of the darter, a bird which requires heavy bones to aid submergence, was only 6.8% of its body weight (Johnsgard 1993).

Possibly on account of their great weight and a tendency to move around on land, the fibula of the pelican's lower leg is unusually stout. Legs and feet, never garishly coloured, are set far back but not enough to inhibit walking, albeit with a nautical roll. In some species courtship involves 'parading'. The two outermost toes are about equal in length and the nail of the third toe, used for scratching, is flanged, though not markedly toothed. The claws are curved. As in cormorants, the webs are placed beneath the eggs for incubation (in sulids on top).

Locomotion

Despite their weight, pelicans are adroit fliers and adequate walkers. They are good swimmers and perch competently. Even the ground nesters can

perch in trees. Notwithstanding their totipalmate webs, perching pelicans oppose the hind-toe to the others. Pelicans fly powerfully, head retracted and heavy bill apparently resting on the upper breast. Like geese they often form lines or wedges, wings beating synchronously, gliding now and then. They soar well, primaries prominently fingered, often spiralling to great heights. Some species seek thermals on which to ascend before setting off on foraging trips or migration. They are too heavy in relation to their flight muscles for sustained flapping flight to be economical but they can maintain flap-and-glide indefinitely. When flying low above the waves the brown pelican 'appears to glide along a breaker in such a manner that the energy born of lively water rather than any muscular energy of their own will carry them for long distances without a single wing-stroke' (Murphy 1936). During a February gale of extraordinary force they seemed totally unperturbed, proceeding up and down the breakers at the height of the storm almost as calmly as in the finest weather. Like cormorants and anhingids, but unlike sulids and tropicbirds, they land on water with lowered feet, often skidding along before settling. They swim buoyantly, floating high with head upright, stroking their webs alternately. A speed of 6 km per hour may be attained. During take-off they kick powerfully, feet together.

On land their stance is upright on bent tarsi, and their rolling gait somewhat laboured. Still, they can traverse stretches of open ground in nesting colonies which would be difficult for cormorants. In slow walking the wings are kept folded but in rapid movement they are opened and may be flapped. They can hop.

Body maintenance

Maintenance behaviour has been best studied in the brown pelican (Schreiber 1977) and this is probably representative of the family (see Vestjens 1977 for Australian pelican). These behaviours, though stereotyped, are unritualized and non-communicatory. Pelicans settle their plumage by shaking, wing-flapping, and tail-wagging. They wing-stretch (including in some species the simultaneous overhead stretch), leg and wing stretch to one side, and

scratch directly (beneath the wing) using the middle claw to rake out feather lice.

Unlike cormorants and frigatebirds, pelican plumage is waterproof and kept so by the secretion of the preen gland which is transferred from the gland to the back of the bird's head and then rubbed onto the plumage. The tip or side of the bill may be used to squeeze oil from the gland (Johnsgard 1993). Pelicans preen, sitting or standing, using the normal range of nibbling, stropping and feather-drawing movements.

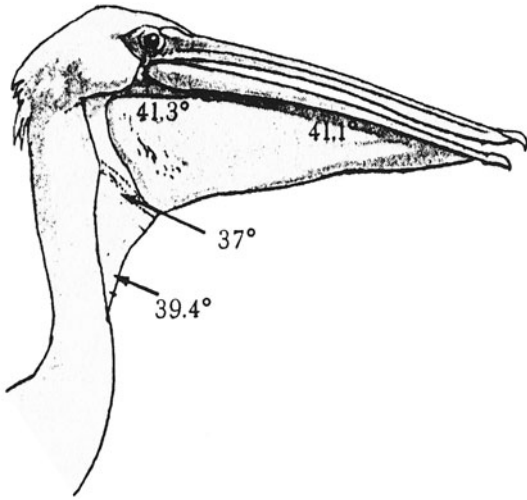
Preening pelicans frequently stretch the pouch by head-up movements, thus rearranging gullet, trachea and air-sacs. In 'glottis exposure' the rami of the lower mandible are bowed outwards, bill open and head lowered. The pouch is then everted by pressing it against the convex curve of the neck. Thus the glottis is exposed. Often, in a more or less continuous movement, the bill is thrown vertically, stretching the gular pouch taut. Schreiber (1977) once saw an adult brown pelican become stuck, with its pouch stretched over its vertically raised head. Bill-throw becomes more frequent and contagious during alarm, just as the comfort movement called 'wing-rattle' does in the gannet. In both cases it seems that a comfort movement preparing the bird for flight (the yawn by loosening the throat and air-sacs and the wing-rattle by loosening flight feathers) has acquired communication value. Pouch eversion may get rid of parasites but Schreiber discounted this.

Often, pelicans plunge their heads into the water, parallel to the surface, and slowly withdraw it, the pouch remaining flaccid.

Pelicans may sleep standing up or sitting, sometimes whilst floating. Usually they tuck their bill into the scapulars but often incline head and bill forwards and down.

They are particularly tolerant of sun. Heat is dissipated by pulsating the gular skin, the enlarged throat pouch rendering this highly effective (Figure 5.2). In great heat they increase access of air to the skin by ruffling body feathers but they do not head-hang nor do adults adopt supine resting positions.

Despite their ability to live in hot climates, great whites can survive extreme cold. Two juveniles (presumably hand-fed) overwintered at a fisherman's



5.2 White pelican regulating its temperature by fluttering its gular skin, creating a flow of moist air; evaporation causes cooling. Ambient temperature 44 C. (From Nelson 1980.)

camp on the Ili delta where the temperature dropped to 30° below zero, though they were slightly frost-bitten.

The Australian pelican collects rainwater by raising its upper mandible to $\approx 60^\circ$ and widening the lower to more than four times the width of the upper; a catchment area of 0.039 m² which can collect nearly 300 cc of water (Vestjens 1970).

Moult

Adults moult twice a year. Before breeding they undergo a partial moult which renews nuptial plumage such as crests, and during or after breeding they lose these features and moult more completely, losing some flight feathers as well as body plumage. As usual in this Order, moult is serially descendent and 'interrupted'. Two or three generations of primary feathers may coexist in the wing, which often appears ragged. In some pelicans, such as the Dalmatian, the post-juvenile moult probably starts late in their first year or in the autumn of their second calendar year. However, Schreiber *et al.* (1989) suggested that the first-year primary moult of the brown pelican was complete and that subsequently it began at two or three points simultaneously, thus

moving into staggered moult or 'Staffelhauser'. In each of these groups of primaries the feathers are moulted from inner to outer.

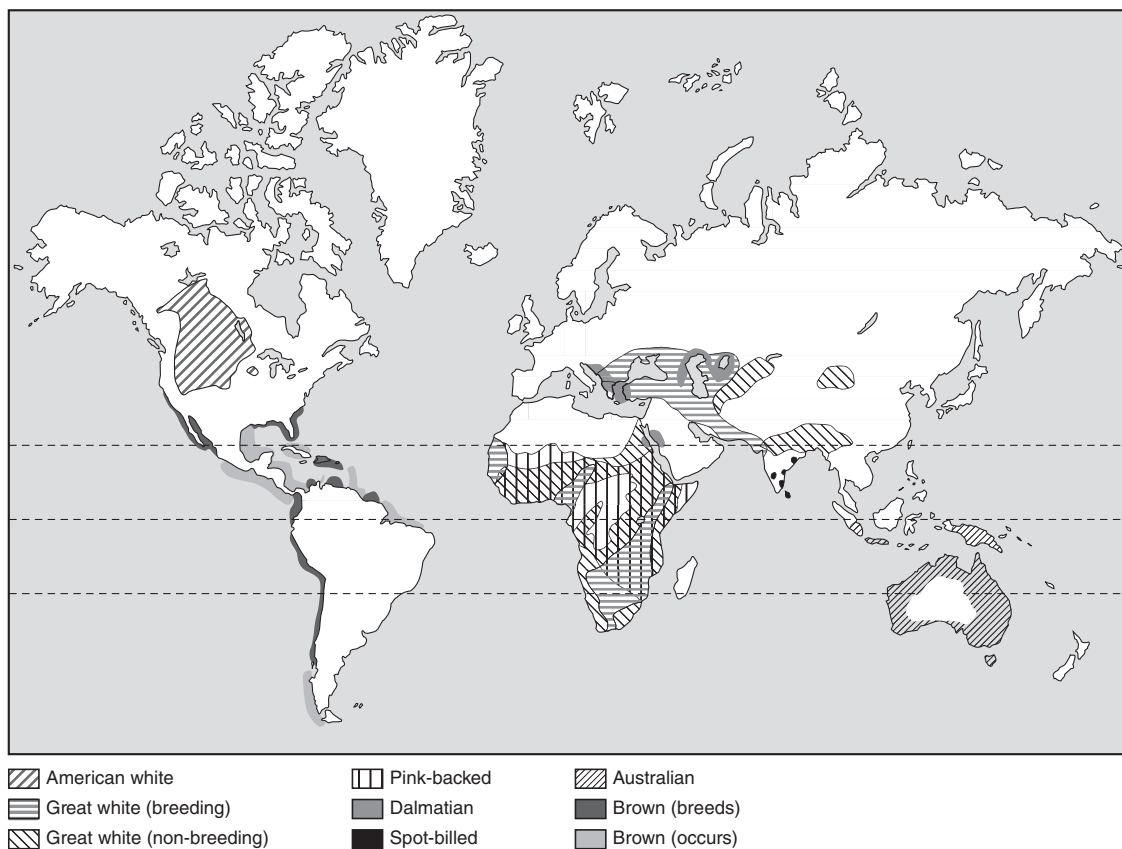
Range and status (Figure 5.3)

Although mainly an old-world family (five species), pelicans occur on all continents except Antarctica and have moved far into the interiors of large land-masses. Essentially warmth-loving (though the great white, at least, is capable of withstanding extreme cold), they are absent from polar regions and, except for the brown, from oceanic islands. Inland South America lacks them. Fossils (Chapter 1) show that they once had a much wider distribution. The Dalmatian was widespread in western Europe including Britain, and New Zealand had its own species. Such changes have been mainly due to man.

Their range is almost cosmopolitan, extending from about 65°N to 40°S and across the world. Within this extensive distribution pelicans have largely avoided overlap, though with notable exceptions such as the great white and Dalmatian in Eurasia and the great white and pink-backed in parts of Africa. Whilst the two latter show marked differences in foraging and breeding habits, this is not the case in the great white and Dalmatian. Here, as in other pelecarniforms such as great and lesser frigatebirds, and tropicbirds, niche-differentiation, whereby species with similar requirements avoid overlap, is a dubious concept.

Johnsgard (1993) suggests that pelicans may have originated in Africa or southern Asia and then spread to northern Asia and eastwards into western North America and south-eastwards to Australia and New Zealand. On this plan the brown pelican would be derived from an ancestral immigrant to the New World rather than the sole survivor of a distinct and primitive line.

The status of the family is described by Crivelli and Schreiber (1984) and updated, particularly with regard to colonies in the USSR, in Crivelli *et al.* (1994). The most endangered species are the Dalmatian, reduced from millions to a world population of 3,125–4,280 breeding pairs; and the spot-billed, now restricted mainly or entirely to Sri Lanka and SE India with a total population



5.3 Distribution of the world's pelican species.

somewhere between 3,000 and 4,000 individuals. Once there were millions in Burma. The most populous pelican appears to be the brown, with more than one-and-a-quarter million birds, largely of the race *thagus* inhabiting the Peruvian guano islands. The Australian pelican (some hundreds of thousands) may be next commonest followed by the American white (maybe 150,000 pairs). The European-Asian population of the great white (as against the African) is considered to be endangered, with somewhere between about 7,000 and 11,000 breeding pairs on 10–13 breeding grounds (Crivelli *et al.* 1994) in the Palearctic. Snow and Perrins (1998) detail only negligible numbers in the western Palearctic. The world population may now have fallen to fewer than 100,000 pairs. Although its population is not known, the pink-backed,

widespread in Africa, primarily south of the Sahara, probably is not threatened.

Outside the breeding season adult pelicans typically disperse or migrate. In the tropics these movements may merge with foraging, which is itself variable as a consequence of major changes in the feeding environment, such as drying up or flooding. Flocks of migrating or dispersing pelicans may contain immature birds but recently fledged young do not typically accompany adults. Juvenile great whites, for example, are largely absent from the preferred feeding areas of adults, though they disperse widely, from some populations at random, for at least 1,000 km. Wide dispersal presumably removes juveniles from competition with adults. Indeed, the same species may be largely resident in one area and migratory in another. South of the

Sahara the great white is a permanent resident, with local movements, but northern populations are partly or wholly migratory, abandoning colder parts in winter. For example, Danube delta breeders depart between September and November and return in March or April (Crivelli *et al.* 1991a). Russian birds depart when freezing begins. Even where basically resident, as in the tropics, the great white may undertake long journeys from one feeding locality to another although such movements are irregular, presumably depending on feeding conditions. Similarly, the American white is partly resident in some areas—that is, some remain and some migrate—but wholly migratory in others, the migration preceded by post-breeding movement away from the colonies and by assembly at favoured gathering places where huge flocks may congregate before gradually breaking up and migrating (Evans and Knopf 1993). Once on the move they may mount high and cross deserts or even mountains. The American white remains almost entirely inland but other species favour coastal movements. The Australian may move along the coast in very large numbers. Occasionally migrating pelicans come down onto foodless lakes and if held there in bad weather may die *en masse*. If food reserves become exhausted by adverse weather and the birds cannot find good feeding, efforts to continue may result in mass mortality. For example, 300 dead and 45 dying great white pelicans were found on a beach near Haifa, probably due to strong winds and unfavourable feeding in the Mediterranean area (Crivelli *et al.* 1991a). Comparable mass deaths are reported for the American white pelican.

No pelicans undertake long sea crossings, although a few stray, or are blown on high-level winds, to oceanic islands. The Australian pelican, for example, is but an extremely rare vagrant to New Zealand and offshore islands such as Christmas Island (IO), Fiji, Pulau and the Solomons. It may be that they eschew sea crossings and the pelagic nomadism which is favoured by sulids, tropicbirds and frigatebirds, because pelicans rely on large concentrations of fish in calm surface layers. Their hunting methods, neither deep-plunging nor pursuit-swimming, could not support their large bodies

if they were restricted to single, perhaps widely spaced food items. Indeed, the brown pelican's post-breeding dispersal northwards along the Pacific coast occurs in association with the movement of prey species such as anchovies, in turn related to changes in the Californian current system. Late in winter, westerlies increase as a result of weather patterns originating in the North Pacific and associated changes in the Californian current may be responsible for the withdrawal of brown pelicans from northern coastal areas (Anderson 1989b). A counter-current with associated upwellings creates favourable feeding conditions in southern California in spring, coincident with breeding, and in summer, with dispersal. In autumn, at least in some years, huge concentrations of pelicans occur along the south coast of California.

Foraging and food

The most important aspects of pelican feeding are:

1. Their ability to exploit distant food sources (cf cormorants) – an unusual feature in an inland fish-eating bird, in some species allowing them to breed on inaccessible sites far from a feeding area. The great white may travel up to 200 km on feeding trips whilst breeding, for example Lake Mikri-Prespa (Greece) (Hatzilacou 1992).
2. The range of feeding behaviours which includes cooperative hunting, piracy and land-based scavenging.
3. The range of feeding habitats, from open sea to inland ditch. The only feeding habitat open to some pelecaniforms but not to any pelican is the offshore pelagic.
4. The ability to catch and transport large meals, which shortens the chick's development time and enables some species to raise more than one chick per brood.

Pelicans which breed in large colonies are crucially dependent on locally abundant food because, unlike pelagic seabirds, they do not have an enormous foraging area. They fly overland to discrete, comparatively small feeding patches. At a daily food intake of 10% of body weight, the Lake Rukwa

(Africa) colony of great whites, at one time *c.* 40,000 pairs, would need almost 17,000 tons of fish during one breeding cycle. Such massive dependence on local food renders them highly vulnerable to shortage and the great white has been known to abandon breeding whilst in full swing. The colony on Lake Natron deserted when *Tilapia* died in astronomical numbers (Din and Eltringham 1974a). Nevertheless, the advantages of breeding in secure fastnesses, even mountainous areas far from abundant food, are considerable and by using thermals to reach reliable and abundant food the journey is economically viable.

The pink-backed pelican nests in traditional rather than opportunistic colonies, containing hundreds or fewer, not necessarily near to water but in trees which secure them against most land predators. They feed a few kilometres away in rivers and lakes and are less vulnerable to local food failure.

The differences in feeding methods between great white and pink-backed pelicans, which may feed and breed in the same areas, have been described by Din and Eltringham (1974b:327). Different feeding methods and prey provide some ecological separation. Like American white, Australian and Dalmatian pelicans, great whites sometimes feed cooperatively. They swim in rows, often driving the fish into shallow water, and eventually plunge their heads beneath the surface to scoop up fish (Figure 6.12). Pink-backs never fish in this concerted manner although they may form loose clusters. The same phases of hunting—searching, trapping, catching and swallowing—are enacted but not in unison. The main difference seems to be that the pink-backed pelican's searching phase lasts some six times as long as the great white's, which may reflect the increased efficiency of group hunting, though only if fish are fairly concentrated. Both species feed mainly from dawn till mid-morning and again at pre-dusk.

The Australian pelican feeds alone or in flocks of up to 2,000. It often cooperates, advancing in loose lines and driving fish into the shallows, where it repeatedly strikes. As it swims the wings are partly extended, possibly shielding against glare. It has been seen to herd ducklings similarly, and even on land may surround and kill young silver gulls (Marchant and Higgins 1990). It will plunge-dive from a metre or two.

The American white forms pre-foraging flocks 'deliberately', birds clearly reacting to others by forming a flock before taking wing. The mechanism of such formation is not known (Sp Acc). They do this even when there are no birds flying past 'directly' or 'purposefully', so information transfer is unlikely to be involved.

The only pelican specializing in plunge-diving is the brown, either singly or in groups which may be huge. Although its dive has been likened to throwing a bundle of washing, it is highly effective. The underwater use of the bill as a massive scoop is shown in Figure 5.4. Juveniles and immatures are less efficient hunters than adults (Sp Acc).

Evidence from captive birds indicates that periods of high intake of food cycle with periods of lower intake, though whether this applies to wild birds is not known. This could conceivably be an adaptation to cyclically varying food if the periods of low intake, with their presumed physiological correlates, corresponded to periods of relative scarcity, though how this could be achieved is unclear.

Pelicans take many fish species (fry to large fish), offal, eggs and young birds, sea-snakes, crustacea, amphibia, etc. (Sp Acc). Most prey is commercially unimportant.

Kleptoparasitism

Pelicans are both victims and perpetrators of piracy. When the fish is tossed up several species of gull try to poach it, even perching on the pelican's head. Belcher's gull may peck at the head or pouch of the Peruvian pelican and grab the fish when the pelican retaliates. If the pelican holds so many fish that it must spill them out and pick them up again the pirates have a good chance. Shealer *et al.* (1997) note that kleptoparasitic gulls and terns are more likely to target and are more successful against adult than juvenile brown pelicans. On the other hand Duffy (1980) recorded the Peruvian pelican pirating guanay cormorants and Peruvian boobies. Either the pelican attacked a booby or cormorant sitting on the water and having difficulty swallowing a fish, or a group of 2 to 20 pelicans settled near to diving boobies and cormorants



5.4 Communal fishing by a group of great white pelicans. (From Nelson 1980, drawing: J.P. Busby.)

and intercepted a surfacing bird, holding it until it regurgitated.

Roosting, loafing, and clubs

Roosting and loafing differ in that the former is mainly sleeping whereas loafing includes preening, digesting food, and generally resting.

Pelican roosts may be large and extremely dense. Peruvian pelicans pack shoulder to shoulder in thousands on sandbars. On the coast of the Caspian Sea, by Sept–Oct, huge groups of Dalmatian and great white pelicans roost on remote spits; great whites roost in single or divided flocks up to 2,000 in a group.

Most pelicans choose open sites such as sandbars, offshore islands, open beaches, or rocky coasts. Trees and bushes may be used by brown, pink-backed and Australian pelicans though only rarely by the great white and apparently never by the American white. Unlike the others, the Peruvian pelican sometimes roosts on water, even well offshore.

Communal roosting and loafing (often with other waterbirds) occupies much of a pelican's time. A brown pelican was inactive for 81% of 24 hours (Croll *et al.* 1986). Similarly, the great white may catch its food in an hour or two of the early morning, spending the rest of the day loafing, bathing and preening. Even in the breeding season there is

a notable dearth of interactive behaviour in such flocks. At the beginning of the breeding season most American white pelican non-breeders return north with the breeders and loaf or roost in the colonies. Within loafing and roosting flocks there seems no segregation by age, sex, or status; groups may contain off-duty birds, failed breeders and non-breeders. Similarly in the great white, unmated adults and pre-breeders roost on the breeding island where they may be joined by parents of large young and even by young birds. But immature Dalmatian pelicans are seldom seen in the colonies although non-breeders in adult plumage frequently spend the summer there (Hatzilacou 1992). Loafing sites of pink-backed pelicans on sandbanks or spits tend to be permanent. Din and Eltringham (1974a) classify nine different types of loafing ground (river, bay, peninsula, island, lagoon, coast, inland pool, emergent dead trees, living trees)—most of which are used also by great whites which congregate in much larger groups.

Outside the breeding season resident pelicans may roost and loaf within the breeding area but roosts are generally distant from the colony and may contain migrants, wintering flocks, or foragers. Migrating flocks drop to roost an hour or two before dark and remain until thermals allow soaring flight after sunrise. On clear, moonlit nights they may go fishing. Brown pelicans show no segregation by age



5.5 (a) Brown pelican plunge-diving (sequence of positions in one bird). (b) Synchronous diving of blue-footed booby compared with (c) Superficial plunge of a tern. (From Nelson 1980, drawing: J.P. Busby.)

or sex in their winter roosts. Australian pelicans may use separate day and night roosts.

Clubs (*sensu* Atlantic gannets q.v.) seem not to occur.

Habitat and breeding biology

Habitat

Typically, pelicans inhabit lakes, rivers, marshes, estuaries, temporarily flooded areas and wet, cultivated land. They require rich feeding areas and in some species, especially the great white, American white and Australian pelicans, breeding areas free from disturbance and predation by large mammals. Because the great white and Australian pelicans may breed opportunistically, sometimes in very large

colonies, to take advantage of food-flushes, their colonies may spring out of nowhere, only to be precipitately abandoned when food runs out. By contrast, the colonies of pink-backed, spot-billed, Dalmatian, and, in some cases, American white pelicans are strongly traditional. Pink-backed and spot-billed pelicans, which are tree-nesters, often breed near to, or within, areas of human habitation.

The five ground-nesters prefer bare or sparsely vegetated, flat, or gently sloping ground, often on small islands in estuaries or lakes. Emergent aquatic vegetation may be used as a base for nests (four species) and trees are used by three species. Only the brown pelican, the single essentially marine species, nests on the most arid rocks, cliffs, and in trees, especially mangroves.

Colonies

All pelicans are colonial and even inland colonies may number tens of thousands of pairs, though far surpassed by those of the Peruvian pelican which are supported by the legions of anchovies in the Humboldt current. In 1919–20 Lobos Afuera held some 50,000 nests and, previously, vastly more. Earlier this century, thousands of brown pelicans bred in the Mississippi delta and seven colonies in the Bay of Panama contained more than 70,000 adults. Great white and Australian pelicans may form large, transitory colonies near to suddenly productive areas, to take full advantage of which these pelicans can breed at any time of year. Some African colonies of great white pelicans may occupy a breeding area throughout the year, new groups replacing old. In such cases, breeding is triggered proximately, by food, as in some tropical boobies. But the north European populations of the great white, as also the Dalmatian and the American white, are seasonal breeders.

Inveterately gregarious, even breeders with ample space may crowd closely. A pelican colony never displays the regular pattern of a gannetry. The groups within a colony, often topographically demarcated, show marked synchrony of laying but sometimes markedly out-of-phase with each other. Mixed colonies, especially of great white and Dalmatians, are common. Often, other waterbirds such as flamingoes, cormorants, storks and ibises mingle with pelicans and the presence of other nesting waterbirds, particularly ciconiiforms, has been known to stimulate reproduction in the wild, as also in captivity. In Tel Aviv zoo the pelicans didn't breed until surrounded by mirrors.

Frequency, timing, and duration of breeding

Breeds annually. As mentioned, pelicans may breed seasonally, extended-seasonally or a-seasonally, depending on climate and food. The cycle is short, partly because pelicans can compress pre-laying preliminaries into a few days. Although opportunistic breeding thus becomes possible, no pelican is known to breed successfully more than once a year.

Territorial behaviour

The ground-nesting great white, Australian and American white markedly resemble each other in several displays, as do the three arboreal pelicans. Pelican displays are clearly related to those of sulids, cormorants and anhingids. Pelican territory is solely the nest and its immediate environs. With the notable exception of the Peruvian pelican, sites are rarely if ever a limiting resource and most pelicans are not faithful to them or to mates in successive breeding attempts.

Site defence grades from jabbing or grappling, to threat, but pelicans seldom fight, and when they do it occurs during communal interactions and is likely to be sexual rather than territorial. During hundreds of observation hours Schreiber (1977) recorded only six fights in the brown pelican. Instead, defending pelicans point or lunge at potential intruders or open the bill and close it with a resounding snap. A 'head-up' display (see figures at end of Chapter 5) is usually interpreted as agonistic behaviour. There is no ritualized site-ownership display and, as in most other pelecaniforms, ritualized behaviour is largely concerned with the pair-relationship.

Pair-formation

Except in the arboreal species (brown, pink-backed and spot-billed) the actual nest-site is not used for sexual advertisement. Pairs are formed elsewhere and the site is then selected. This system differs markedly from that in most pelecaniforms in which the male competes for and establishes a site on which he then displays to females. However, some cormorants (for example the European shag and flightless cormorant) may interact away from the site, the male then leading the female to it, so it seems that the pelicans have retained more of this (presumably more primitive) method. Pairs form at or near the colony and not, so far as is known, in winter quarters or on migration, or in clubs or loafing areas. The communal interactions, chases and processions which take place on land or water, or in the air, either in all-male groups or in mixed-sex ones, have no counterpart elsewhere in the pelecaniforms, or even in any other seabird. The unique and complicated communal interactions, nowhere adequately

analysed, seem to have the following elements: a group, usually more males than females, or even, at first, entirely males, engages in a variable sequence of activities which may include circling flights, swimming parties, ritualized walking ('strutting') and chasing. Within each of these activities certain stereotyped displays occur. For example, within the colony, Australian pelicans (Vestjens 1977) come together in a small, mixed-sex group in which males predominate. By means which have not been described, a female attracts a number of males who then follow her, on foot, by swimming or by flying, sometimes all three in sequence. Males interact with each other ('pointing', 'gaping' and 'thrusting') and they ripple their pouch, the waves moving from throat to tip of bill whilst simultaneously the upper mandible moves up and down in a clapping motion which produces audible 'clunks' running together in a rattle. The pouch is swung from side to side with the bill open and the neck stretched vertically whilst at the same time the bill is moved slowly up and down. In the great white pelican (Brown and Urban 1969), males thrust their bills into the centre of the group, occasionally interlocking them, reminiscent of communal fishing. Eventually individual females are pursued by one or more males but finally only one male persists. Why the others abdicate is not described. There is no obvious indication that the female selects him from the original bunch of suitors and his success presumably depends on the outcome of his interactions with the other males although, possibly, the female has reacted differently to him. If the interactions were on water the pair then land and with a strutting walk, heads held high, wings partly spread and pouch rippling, move either to a nest-site (female leading) or eventually rejoin a displaying group. Homologous behaviours are present in the American white (Sp Acc). Amazingly, the entire, complex procedure of pair-formation can, it appears, be completed in one day.

Procedures are substantially different in the tree-nesting pink-backed pelican. There is less group interaction although parties may fly from tree to tree and interlock bills *en masse*. Din and Eltringham (1974b) saw 20 birds do so, which suggests that this action is not overt fighting but the arboreal equivalent of the similar behaviour described above. Males

are said to advertise (sexual display) by 'throwback' in a manner strikingly resembling the equivalent behaviour in the spot-billed pelican and the cormorants, anhingids and boobies.

The arboreal brown pelican lacks communal display as a prelude to male advertising. Schreiber's (1977) detailed account makes no mention of such a phase and begins with the unmated male's behaviour in selecting and occupying a nest-site in mangroves, where he performs a ritualized head-swaying (see Sp Acc). This seems equivalent to the pink-back's throw-back and, like it, is performed also by male and female together during interactions on the nest. It is thus both an advertising and a pair-bonding display. When performed by the unmated male the gular pouch is fluttered, seemingly akin to pouch-rippling in other pelicans where, also, it is courtship behaviour. Among the stimuli which elicit an increase in pouch rippling are the approach, in flight, of another pelican, the proximity of courting pairs and the landing nearby of a female. Lone females on the nest do not perform this display. Interestingly, the peripatetic element so typical of pelecaniform courtship is not entirely absent in the brown, for the male periodically flies out from his site, circles and returns. Most males succeed in attracting a female within two to four days, sometimes within a few hours, in which case the renewal of a previous bond may be suspected. During this early phase partners remain on the site almost continuously and do not feed, though this can hardly be true for males that take two or three weeks. The female thus selects male-plus-site. The presence of perches nearby may be important.

Pair-bonding

Some of the displays used in pair-formation continue as pair-bonding behaviour, reflecting the fact that the two phases are a continuum (see brown pelican). The period of mutual display quickly wanes, probably as partners learn to recognize each other, though the 'in' bird may continue to display in response to each approach of the partner, just as some cormorants continue a version of their advertising under similar circumstances. Bonding

displays which appear to be homologous include 'head-turning' or 'pouch swinging', 'head-swaying' and 'bowing' (Sp Acc).

When a female joins a male on his site, as in the brown pelican, he may be aggressive enough to bar her from the site or even the adjacent perch. She lacks obvious appeasement behaviour but maintains eye contact. This early period of direct contact is nervous and tense and much time is spent standing and looking at each other.

Copulation (Figure 5.6)

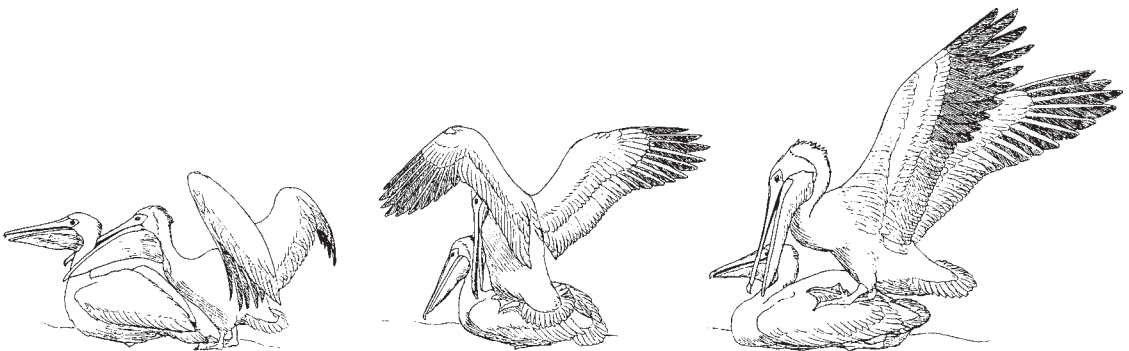
Begins 3–10 days before egg-laying, sometimes within hours of the partners coming together. It may occur several times per hour, most commonly (spot-billed) in the afternoon. Whilst most pelicans mate on the nest-site, some ground-nesters attempt it during prior courtship—even (great white) on the water, though unsuccessfully. It is preceded by display. The Dalmatian and Australian male (at least) swivel raised wings by rotating the humerus (reminiscent of the sexual advertising in many cormorants, anhingids and boobies) whilst crouching with rump and tail raised. But in the brown pelican there is no ritualized precursor. Female pelicans squat. The male grasps the female's neck (but may merely place his bill alongside during mating) and mounts from the side or behind (Schreiber 1977, for brown, notes mating is successful only after

mounting from behind). He opens and beats his wings (all species) and, at least in some, treads (pink-backed, American white). The female also partly opens her wings. The time taken varies, partly depending on criteria; from actual mounting 5–10 seconds. The male rubs his cloaca with increasing speed against the female's and grunts harshly. After dismounting all male pelicans perform comfort behaviour such as wing-flapping, tail-wagging, pouch eversion, gaping and preening. They alternate copulation with bringing nest material. Copulation ceases abruptly after the last egg has been laid which saves energy and prevents egg breakage. Extra-pair copulation is common in the great white, pink-backed, and Dalmatian, and occurs in the spot-billed, but is apparently rare or unrecorded in American white and brown. Reverse copulation seems unrecorded.

Nest

Building becomes part of a sequence in which trips for nest material are interspersed with copulation. Nest-building movements, and the structure itself, probably influences the female's physiology since, in the brown pelican, the first egg is laid 1–3 days after the completion of the nest even though building time is variable.

Ground-nesting pelicans may build little or no nest. Great white and Australian pelicans lay their



5.6 Copulation in the brown pelican. (From Johnsgard 1993, after Schreiber 1977.)

heads sideways and shovel up substrate, creating a hollow whose rim might later be embellished with stones etc. The male great white, but never the female, may walk to vegetation and tear some off, or uproot grass using a sideways wrench. The material is stored in the pouch until it bulges 'like a sack full of rubbish', whereupon the male disgorges it in front of the female. Apparently he does not fly off for material, unlike the Australian which, despite collecting as many as 2,000 items, may fly a kilometre for a single one. This adaptable pelican will trample bushes to make a nesting platform or use its feet to push sand backwards, having first loosened it by digging with its bill. It scrapes with one foot at a time, rotating and changing feet every few seconds. The arboreal pink-back and the brown do not pouch material but carry it crosswise in the bill. It might be awkward or dangerous to pouch sharp material such as twigs. The juggling movements by which brown pelicans adjust twigs for flying trim has become ritualized in some boobies into a display in which even a symbolic scrap is swung in a high arc. Some cormorants, similarly, use presentation of material as bonding behaviour. Twig-using pelicans manipulate them into position, jerking their wings for leverage. Females do most of the building but males may assist. A substantial nest takes 4–10 days to build. The nests of pelicans may be so close that they form a communal platform; pink-backs, at least, actually in bodily contact. Their nests and excreta may eventually kill the tree. Tossing nest material (and incidentally unattended eggs and small chicks), has been observed in several pelicans and is probably a displacement activity, ethologically and literally!

Egg/clutch

All pelican eggs are approximately sub-elliptical to oval, coarsely textured, dull white overlain with a chalky coat which stains and roughens. Clutches are most commonly two, though often three. Larger clutches probably involve more than one female. The intervals between successive eggs varies with species and in pelicans is longest in those most given to siblicide.

Pesticides left harmful concentrations of DDT, DDE and hexachlorine cyclohexane in great white pelican eggs and chicks in the Ili delta (1988–89);

levels were more than 10 times those in fish and probably killed some young (Zhatkanbayev 1994a). Pesticides are used heavily in Africa, though no eggshell thinning has yet been described. For the brown pelican Blus (1982) established the critical level of DDE in eggs as 3ppm (fresh, wet weight), above which shell thickness decreased by 18–20% and some eggs broke. Blus *et al.* (1997) confirmed this shell-thinning and added that the mass and shape of eggs is not affected. Schreiber and Riseborough (1972) gave detailed figures for pollutants in this pelican. In the American white, eggshell thickness decreased from 0.686 mm ($n=58$) before 1940 to 0.620 ($n=100$) in 1972, linked to levels of DDE and DDE + TDE (see Evans and Knopf 1993 and references). Crivelli *et al.* (1989) analysed eggs of the Dalmatian pelican from Greece (1984–86) and found low concentrations of residues of trace elements and PCBs but high ones of DDE. Shells were only 0.483–0.800 mm thick compared with a pre-1947 mean of 0.734 mm. (See Chapter 4.)

Replacement laying

Lost clutches may be replaced (Sp Acc).

Incubation

Pelicans place eggs on top of webs or beneath them, presumably depending on ambient temperature. The sexes share incubation more or less equally, changing over about daily within a range of three hours to three days depending on species and locality. Early in incubation, display at change-over is conspicuous but towards the end, partners may change-over without ceremony. American whites perform the 'head-up' and the 'bow' several times, with a nasal 'ho, ho, ho', whilst interspersing nest-material handling and displacement preening. The great white alights and walks to a place nearest to its nest before threading through neighbours which lunge and peck. It then performs the 'head-up' and the 'bow', which is largely associated with nest-relief. The incomer approaches with partly opened wings and raised bill whilst the bird to be relieved backs slowly off, sometimes in the 'head-up' position, sometimes with bill tucked (this is the 'bow' of Brown and Urban 1969).

The pink-back has a conspicuous display ('head-bobbing') apparently specifically concerned with partner-recognition, which Burke and Brown (1970) strangely do not mention, although Din and Eltringham (1974b) considered it to be part of nest-relief. In addition, the main pair-formation display ('bill-clapping') is sometimes associated with nest-relief.

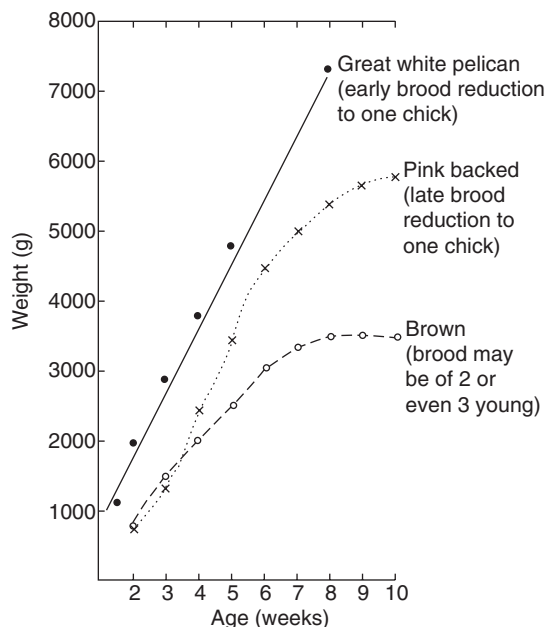
During incubation most of the pelican's time is spent resting, sleeping or preening. The site is defended by 'pointing', jabbing and bill-snapping. In the American white this may become audible sparring and bill-locking, with nasal growls. Colonies are often noisy and fractious.

Periodically, incubating birds shift an egg by inserting the bill-tip beneath it and rolling it towards the feet which are then repositioned; the bird uses one wing to balance whilst raising the opposite foot. Nests may be temporarily vacated and eggs are then vulnerable to predation. This neglect is difficult to interpret but ground-nesters are easily deterred from incubation. Mildly disturbed great whites walk away and on return, which may take some hours, stand around uncertainly. The readiness with which some pelicans desert their colonies may be another indication of this weak attachment to site. In opportunistic breeders this may be the price paid for the benefits accruing from the ability to start and stop cycles quickly in response to environmental stimuli. Spot-billed and pink-backed pelicans, on the other hand, are much less wary. Their colonies are traditional rather than opportunistic and they are accustomed to man.

The incubation period is 28–35 days (extremes), varying *within* species by about three days. It is thus short, mainly 31–33 days, as it is in cormorants but not in pelagic peleceniforms. Consequently the hatchlings are small and weak and find difficulty feeding from such a large parent, despite special procedures (Sp Acc).

Chick, brood, and brood reduction

Chick down may be white, grey or dark brown and grows in less than two weeks. A complete plumage of true feathers is acquired in two months. Growth is rapid (Figure 5.7).



5.7 Pelican growth rates; individual chicks.

Like sulids, cormorants, and anhingids, some pelicans can rear more than one chick per brood. But the Australian, great white and pink-backed are not known to do so and even though all pelicans lay clutches of two or more, most species raise only one chick. The most likely to raise two are the brown and spot-billed, though American white and Dalmatian may do so. This marked tendency for brood reduction is consistent with quickly rearing a large biomass.

Optimal brood-size can be achieved by immediate siblicide (Sp Acc) or by competition for food leading in some instances to the demise of the weakest.

Care of young

Shared about equally. Naked young need protection from sun. The body temperature of unshielded brown pelican chicks increased by 3°C in a few minutes (Bartholomew and Dawson 1954). At night, the temperature of such young soon dropped to around air temperature, though even when body temperature was *c.* 20°C below daytime resting level, they were not torpid. Chicks are closely

brooded for the first 10–14 days and night brooding persists for a further fortnight or so. During the second fortnight adults may stand over, or to one side of, the young. The shade which they provide by turning their backs to the sun and partly spreading their wings seems not deliberately orientated for the benefit of the chick, though the latter may seek it. Several young may cluster in the shade of one adult thus, as Brown and Urban (1969) remark, beginning pod-formation, which may be largely thermoregulatory. After that, young pelicans may be unattended day and night. At this stage they may begin to form true pods (see later).

Like most pelecyaniforms, pelicans have difficulty in feeding newly hatched young and until the end of close-brooding, chicks are stimulated to feed. It is difficult to see what they do to tiny young but large chicks may be treated extremely roughly. The great white chick is seized by the neck and shaken and may be flung about. Young birds may be hauled out of a pod and manhandled prior to feeding; such rough behaviour has not yet been convincingly interpreted.

Even after brooding for 48 hours, adults can still regurgitate. The methods used to deliver food are unusually varied. The Australian positions its bill nearly vertically and the chick sips from the tip the liquid that dribbles down the inside of the upper mandible. The great white pelican presents its bill upside down; the red nail at the tip of the upper mandible may stimulate the chick to peck at it and take the semi-liquid from the groove. The American pelican points its slightly open bill into the nest and regurgitates small, semi-digested fragments into its partly-spread pouch, though the young feed from the tip of the lower mandible (Schaller 1964). Probably all pelicans feed their tiny young by regurgitating partly digested fish into the nest (Din and Eltringham 1974b, Grummt 1984). The phylogenetically primitive Abbott's booby is the only other pelecyaniform to use this method. Later, the young become progressively more versatile in extracting food. They may even stand in the adult's pouch.

The adult's posture when delivering food depends on the age of the young. When feeding large young the parent squats on its breast and stretches the head and neck forwards. After the chick has inserted its

head and neck the adult may be forced to stagger around until it can shake itself loose.

Parents feed only their own young even when these are in pods. Young Australian pelicans will not even beg to non-parents (Marchant and Higgins 1990). Recognition is mutual and apparently is based on sight rather than sound. Brown and Urban (1969) describe great white pelicans searching a pod for their young and chicks rushing out to solicit. Failing this, adults inspect another pod. Strange young are repelled by vigorous jabbing. Marked individual chicks of the American white proved to be fed by two adults only. At least when nesting in trees (and unlike the equally arboreal pink-backed), brown pelicans will not feed their young away from their site.

Some species bring water to their chicks as, also, do some cormorants though not sulids. Perhaps this trait relates to the habit of some pelicans and cormorants of breeding in extremely hot inland regions.

Behaviour of young

Begging (Figure 5.9)

During their first six weeks, after they have been stimulated to feed by their parents and even hauled out of pods, young pelicans peck at the adult's beak and breast. Later they seek their parents without prior treatment and are often violently importunate.

Pelican chicks may fall into convulsions before or after feeding. During this bizarre behaviour the chick violently bites its own wing or leg, throws itself to the ground, thrashes around and may lie comatose. In pre-feeding convulsions the American white may attack other young. Cash and Evans (1987) note that convulsions or attacks occurred in 90% of all feedings of chicks aged three weeks or more. In this species chicks that had to beg longer were more likely to show convulsions and aggression. The Australian, which often convulses after feeding, lies comatose for 30 seconds and then stands up and acts normally (Vestjens 1977). In nests with two chicks, apparently only the larger convulses, mainly after the first of two feeds. Its convulsions prevent the younger from feeding and the sibling starves. Convulsions occur right up to the last parental feed. In the pink-backed, Burke



5.8 Creche or pod of chicks of the Australian pelican. (Photo: J. Warham.)

and Brown (1970) described 'crazed fighting of other young, branch biting and biting of their own wings'. Afterwards they may collapse and lie as though dead. Nagulu (1984) says the spot-billed head-swags, beats wings, bites twigs or its own wings, jerking violently right and left (strikingly like Abbott's booby display). Replete ones may collapse for some minutes. Convulsions occur, also, in the great white pelican. Presumably they occur in the Dalmatian, which resembles the Australian, great white, and American white in many ways. I cannot find explicit descriptions of this behaviour for the brown pelican.

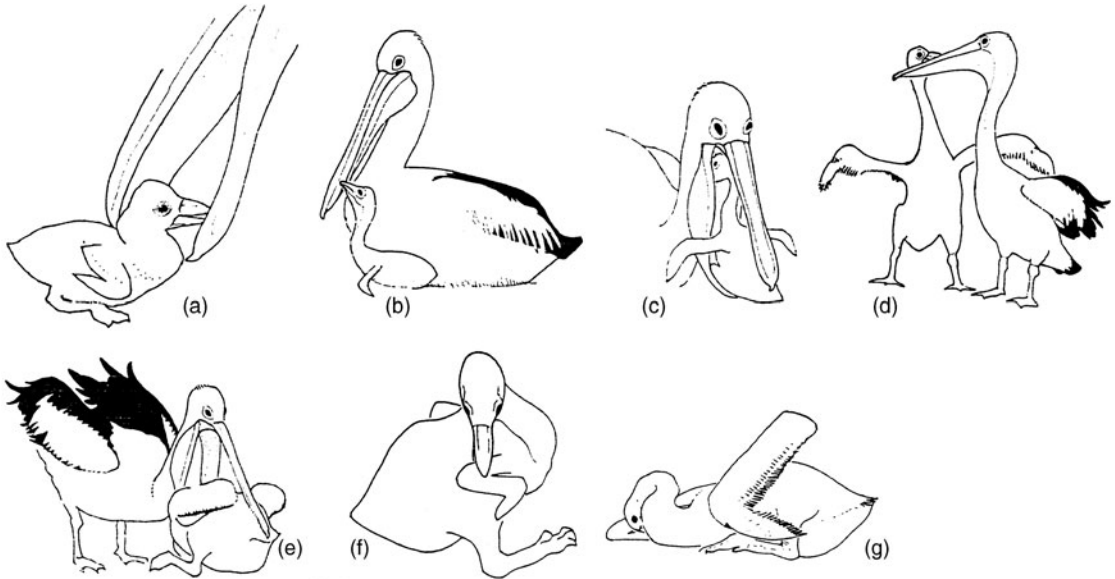
The interpretations are either partial or unconvincing. Nagulu suggests asphyxiation as a consequence of having its head deep in the adult's pouch for four or five minutes, or after swallowing an unusually large fish. This does not explain pre-feeding convulsions. Cash and Evans (1987) suggest that it is hypertrophied begging and an attempt to drive other young away. Displacing potential competitors would seem unnecessary in single-chick species in which adults can recognize their own young and convulsions would in any case be highly inefficient.

Resting, sleeping, and thermoregulation

Whilst still downy, young pelicans sit or lie with head on the nest or ground. They dissipate heat by panting and gular fluttering, providing a large, bare surface area for evaporative cooling which may be important in this family's ability to tolerate extreme heat. Several young may shelter in the shade of an adult. Pods play an important part in heat control (see 'crèching' below).

Sibling rivalry

All pelicans lay clutches of more than one egg but the loss of the second and third chicks is common if not, in some species, universal, although in others (Dalmatian, American white, brown, and spot-billed) two chicks may be reared and some brown pelicans may rear three. Siblicide is recorded for the great white (Cooper 1980), pink-backed (Din and Eltringham 1974b), Australian (Vestjens 1977), and American white (Schaller 1964). Of these, only the American white manages, in a small but significant proportion of cases, to raise two chicks to fledging stage. In the great white pelicans of Dassen Island, half of the nests held broods of two, but only where



5.9 Australian pelican chick-feeding technique: (a) feeding from tip of upper mandible (b) begging (2 weeks old) (c) feeding (d) begging posture (large young) (e) feeding (f) self-biting during convulsion (g) collapse during convulsion. (From Vestjens 1977.)

both chicks were less than three days old (Cooper 1980). Where one chick was older than this the sibling was dead, with extensive wounds on the head. Larger chicks were seen to crawl towards their sibling and attack it. In one case, where the younger chick was still partly within the eggshell, its sibling pecked at the exposed pink body even though the head had not emerged. Even chicks that could barely raise their heads attacked their sibling. However, Brown and Urban (1969) did not record fatal aggression in this pelican, though Vesey-Fitzgerald (1957) had done so at Lake Rukwa. Brood reduction due to the exclusion from food of the smaller chick has been noted in the brown pelican, perhaps especially in bad years. In good ones, broods of two or three survive. In the spot-billed pelican there is high mortality of the second chick (Neelakantan 1949), apparently from starvation. Often, in the pink-backed the larger sibling attacks the smaller. There is considerable mortality between weeks three and seven and even chicks as old as eight or nine weeks may be driven from the nest and end up in awkward or fatal posi-

tions among the branches. If they fall to the ground they are not fed.

Pelicans adopt the same mechanisms, that is obligative and facultative reduction, as boobies, whereas in cormorants only indirect, facultative reduction occurs. No pelican has adopted the sullen strategy of restricting the clutch to one.

Reactions to neighbours

In ground-nesters, large young have been known to cannibalize small ones, though whether the latter were already dead or dying and whether the colony had first been disturbed is not recorded. On the other hand, young pelicans are highly gregarious, ground-nesters congregating in pods, and in species where nests may be contiguous, such as some Dalmatian and great white in reed beds and pink-backed in trees, neighbouring chicks presumably coexist amicably, though with occasional sparring. There are discrepancies in accounts of the reactions of chicks to non-parent adults. Some say that chicks will beg to them whilst the young Australian is said not to approach them.

Crèching

Mobile young of ground-nesting pelicans gather in pods. In the great white, chicks of 14–28 days gather in small groups of up to 5, growing to about 30. Later, groups of up to 100 or more may form. At this stage they take to the water if disturbed. They recognize their parents and leave the pod to beg for food. Between about 6 and 8 weeks the young wander around more freely and large pods break up. The young birds move to the water's edge and swim more readily. At 7–10 weeks they become free-swimming and, in the later stages, begin to fly. The American white seems less prone to congregate into early pods, at first forming only very small groups which break up easily, especially at night, when the chicks may return to be brooded. Usually, they do not join a pod until they are about a month old and no longer brooded. Pelican pods grow in size during the day. Around midday, young pelicans appear torpid, resting on their tarsi and fluttering their gular sacs. Pods shift position to avoid strong wind but chicks return to the original pod-area to be fed. Whilst pods help young to conserve heat at night, Brown and Urban (1969) comment that at Lake Shala they did not increase in size in response to cool conditions but did so in response to midday heat. Large groups broke up in the cool early morning but reformed as the day grew hotter, presumably because individuals in tight pods expose less surface area. The tendency to form pods is clearly a definite stage in development. Many young phalacrocoracids tend to form groups but these are much less organized, and looser, than in pelicans. In the American white, once pods begin to form, adults which are still incubating or brooding tend to abandon their nests and join loafing adults (Schaller 1964), although this exposes their eggs or small young to predation. In the great white pelicans of Lake Shala, where the colony may contain breeding birds at all stages, such desertion did not occur.

Fledging

Pelicans grow quickly on frequent, large feeds, achieving flight in 10–12 weeks or less compared to 24 weeks in frigatebirds and Abbott's booby.

Ground-nesters achieve flight gradually, exercising their wings before taking short flights, stimulated by gusty winds. At this stage the young has lost weight through feather growth and because it is receiving less food. Young great whites have practised communal fishing even before they can fly, and are presumably independent thereafter. The tree-nesting pink-backed graduates from wing-aided hops within the tree to more extended flights, landing in trees which are sometimes hundreds of yards from its own but often returning.

Post-fledging

Young which remain in the colony may continue to be fed; pink-backed for two or three weeks. Others appear to linger nearby, roosting and loafing with adults whilst some species (or perhaps populations) leave the colony soon after they can fly. Although some authors describe parental care as 'prolonged', it is not so when the biomass of the young is considered, nor when compared with prolonged care in some other pelecaniforms such as frigatebirds, some sulids, and some cormorants. Young brown pelicans, once flown, do not return to the nest and are not fed away from it (Schreiber 1976a), nor can they have practised feeding beforehand.

Breeding success

Excluding disturbance and desertion, pelican hatching success is variable but potentially extremely high (up to: 96% in the great white, 90% in the brown, 95% pink-backed, and 91% in the American white). Factors include clutch-size, age of female and (in seasonal breeders) the time of year at which the clutch is laid.

Fledging success (fledged from hatched) is variable, usually significantly below 50% but can be around 75%. It is much influenced by the age/experience of the parents and by the degree of siblicide. Experienced female brown pelicans reared 0.9 fledglings per breeding attempt whilst inexperienced birds raised only 0.1 young, partly due to lower clutch-size and later laying but mainly due to poorer rearing ability (Blus and Keahy 1978). The most significant feature of productivity in pelicans is its inconsistency. Flooding, desertion after food

failure, disturbance, inclement weather and infestation by ticks can cause severe losses. Even under favourable circumstances productivity rarely reaches an average of much more than one fledgling per pair. Pelicans may not breed every year and recruitment must be further reduced by losses resulting from the absence of post-fledging feeding. Therefore, compared with cormorants, pelicans are rather low producers, even with their huge food-gathering capacities and clutches of two or three eggs. On the other hand they have a fairly short deferred-breeding period, and during their breeding life may experience one or two exceptionally productive breeding cycles.

Fidelity to colony, site and mate

Pelicans combine an attachment to certain traditional breeding areas, such as a lake (American white, Dalmatian, some great white), a delta (Dalmatian and great white), a particular mangrove swamp (brown pelican), a clump of trees (pink-backed, spot-billed), or an island (brown pelican), with a readiness to shift the location of the colony within the general breeding area. The Australian and great white may colonize entirely new areas for one or two breeding attempts and then abandon them. Where there are several colonies of brown within a generalized area, as in the Gulf of California, individual pelicans may change their colony in successive breeding attempts (Anderson and Gress 1983). In general, pelicans do not maintain their sites or mates for more than the one breeding attempt, although longer-lived attachments almost certainly occur. Natal philopatry is likely to play a significant role in traditional colonies, but such colonies may be the exception rather than the rule.

Age at first breeding

Usually three or four years but, especially in the brown pelican, occasionally only two.

Non-breeding years

Nothing is recorded about the correlates of non-breeding in apparently adult pelicans, nor about the

proportion of such individuals within or near to a breeding colony (Chapter 3). But some colonies contain many non-breeders, status unknown but apparently adult.

Longevity and mortality

Wild birds seem not particularly long-lived, the oldest known being an American white of at least 26.5 years. However, captives have lived 41+ years (great white), 40+ (Dalmatian) and 60 (Australian). Great whites were still breeding at 32. Annual adult mortality figures are not available for all species but for the brown is *c.* 18% and for pink-backed *c.* 13%.

Causes of death

(See Chapter 4.) Mortality, often linked to man, results from predation by large mammals (lion, boar, hyaena, leopard, dog, fox, coyote) and large raptors. Mass mortality can occur if migrating pelicans (mainly great white) are stranded by weather; in Greece in severe weather, starvation was implicated in heavy mortality in wintering Dalmatian pelicans (infested with parasites especially *Contra-caecum* in up to 875 per carcass) (Pyrovetsi and Papazahariadou 1995). The parasite load (nematodes, trematodes, cestodes, acantho-cephalans, hippoboscids and their mites) found in many piscivorous birds, occurs in pelicans but (usually) sublethally (e.g. Mhaisan 1994).

Epizootic disease occasionally kills. Newcastle virus caused heavy mortality in American white pelicans in Minnesota and North Dakota in 1992 (Glaser *et al.* 1999), although the cause of an estimated further 5,000 deaths was unclear. Yetan epidemic in double-crested cormorants in Saskatchewan, 1995, left pelicans untouched despite close contact (Kuiken *et al.* 1998). Off Baja California, 1996, massive mortality in brown pelicans resulted from feeding on mackerel (*Scomber japonicus*) contaminated by domoic acid-producing diatoms (*Pseudonitzschia*) (Beltran *et al.* 1997; see Buck *et al.* 1992; Fritz *et al.* 1992; Hatfield *et al.* 1994—latter provides analytical method for detecting this neurotoxin).

Gannets and Boobies

Introduction

Gannets and boobies are marine plunge-divers, able to forage well offshore. They occupy an almost-exclusive feeding niche; cormorants and anhingids are limited to inshore waters and the plethora of offshore tropical seabirds such as terns, frigatebirds and shearwaters cannot dive deeply. The sulids which exploit the same food-rich upwellings, such as the Humboldt, Benguela and Californian current systems, as some cormorants, pelicans, and others do not forage so far offshore. Tropicbirds, which dive deeply and range offshore, are largely solitary feeders and unlikely to be significant competitors.

Sulids nest in many habitats from the flat bottom of a stiflingly hot volcanic crater (blue-footed boobies on Daphne, Galapagos) to precipitous cliffs of sub-Arctic islands, and from near ground-level shrubs (red-footed boobies) to the canopy of tropical rainforest (Abbott's booby). This ability has given them an extensive distribution and, until recently, a large world population. Some sulid species breed annually and seasonally, others non-annually (seasonally or a-seasonally) either more or less often than once a year. And there are considerable variations in breeding biology, such as clutch and brood-size.

They have evolved an extensive repertoire of ritualized display in the context of territory and pair-interactions. Some sulid displays strongly resemble those of cormorants, the family to which they are most closely related.

Classification

(See Chapter 1.) The extant sulids are divisible into three genera: *Morus* with three allospecies; *Sula* with five species (*S. sula*, *S. leucogaster*, *S. dactylatra*, *S. nebouxii* and *S. variegata*) and *Papasula* containing just *P. abbotti*. Recent work justifies the new genus for Abbott's booby and palaeobiologists seem to agree that the three gannets *Morus* should be distinguished from the boobies *Sula*—the differences go back at least as far as the Miocene. Here, the gannets are treated as three allospecies within a

single superspecies (Sp Acc). Chapter 1 considers booby relationships.

The bird

Voice

Sulid vocalizations resemble those of cormorants with a comparable tendency towards sexual dimorphism and an even wider variety of sounds, ranging from bull-like bellows (Abbott's booby—probably why it was called *Le Boeuf*) to thin, piping whistles (blue-footed booby). In between are raucous shouts, quacks, sonorous 'a-arks', soft groans and glottal clicks. Only in Abbott's booby and the Atlantic gannet is there no detectable difference in voice between the sexes, though in the others the degree of difference varies. Male voices are higher-pitched than female.

Vocalizations are largely restricted to interactions at the colony and to communal fishing. Fighting, threat and much display is accompanied by calling but only the red-foot has a special vocalization during copulation. Sexual interactions such as 'advertising', 'greeting' and intimate, on-site behaviour involve vocalization. In large, dense colonies such as those of the gannet, the noise may help to mature the gonads, thus affecting the timing and synchronization of breeding.

During fishing 'frenzies' sulids call loudly, but it would be difficult to show that this is adaptive. However the special vocalization by which cooperative diving is triggered in the blue-foot is presumably adaptive though not known to occur in other species (but see Atlantic gannet Sp Acc).

When begging for food, very young sulids utter typically peleciform, high-pitched 'yipping' noises which become deeper and louder as the chicks grow. Abbott's booby's begging call, like the adult's voice, is distinctive (see Sp Acc). Where there is marked sexual dimorphism in adult voice, the juvenile possesses a female-type voice which may endure for two or three years, presumably until the necessary modification of the syrinx has occurred (Murphy 1936).

Probably in all sulids, mates recognize each other's voice, and chicks their parents'. Neighbours, too, are recognized and play-back shows that the Atlantic gannet, at least, reacts differently

to incoming strangers than to neighbours, using amplitude differences as cues.

External features and anatomy

In all boobies, but especially the blue-footed, red-footed and brown, the female is larger than the male, but in the gannets there is little difference. However, in all sulids the sexes are similar in plumage though some differ in the colour of soft parts and bill, and the blue-foot has a curious difference in the pigmentation of the iris. Characteristically, sulids are mainly white with black flight feathers, or white beneath and brown above, giving rise to several combinations, shown in the colour plates and legends. Gannets and white-morph red-footed boobies have golden-buff heads which turn paler in females as the season progresses.

Only red-footed and brown boobies exhibit marked regional variation in plumage, although the masked booby varies in the colour of the soft parts. The functional significance of the extraordinarily different morphs of the red-footed and brown boobies is not known. Possibly brown-morph red-footed boobies hunt more at night than the white forms. Once adult plumage has been attained it varies little between breeding and non-breeding, though there may be abrasion and fading.

The difference between adult and juvenile plumages runs the gamut from totally different (adult white, juvenile black) in the Atlantic gannet to juvenile and adult male indistinguishable (Abbott's booby). In general juveniles are brown or brown-and-white, with dull bills, face, eyes and feet. All juveniles except those of the Atlantic gannet and red-footed booby have mostly white ventral surfaces (hunting camouflage). Adult plumage is attained between years three and five but gradually, rather than, as in some raptors, straight from a fully immature plumage.

Sulids have a streamlined torpedo-shaped and somewhat ventrally flattened body, longish, graduated, and pointed tail, fairly short neck, forward-projecting head with pointed bill and long, narrow, and slightly angled wings. The flight muscles are comparatively small (about 13% of

body-weight in the Atlantic gannet) and wing-loading high. To fly far and fast with these characteristics the body benefits from low drag. The proportions of the wing vary with species. The upper arm (humerus) is longer in proportion to the forearm in Abbott's booby and the three gannets than in the other sulids. The shape and length of the tail also varies and is particularly long in the acrobatic male blue-foot.

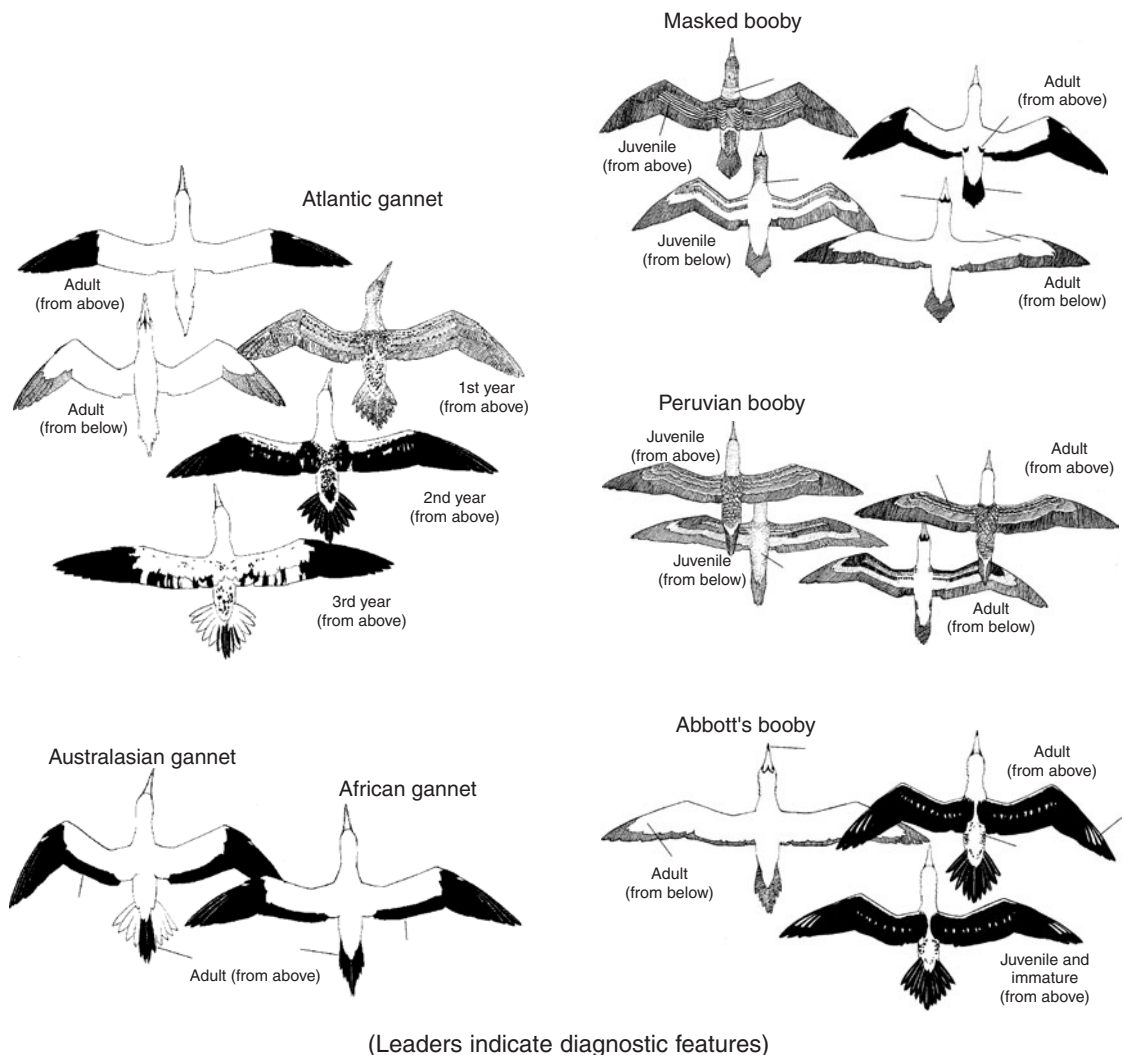
There are 11 primaries of which the outermost (11th) is minute and either 9 or 10 is longest. The aftershaft is vestigial or absent. Tail feathers number between 12 and 18 (not 12–16 as in some texts).

Morphology relates to feeding and foraging (see Hertel and Ballance 1999 for an analysis of 'wing ecomorphology' in seabirds). All sulids have high-aspect-ratio wings but flight and diving abilities vary with overall size, weight, wing-proportions and tail-length. A male blue-footed booby, small, light, long-tailed and with a comparatively short upper-arm in relation to forearm, contrasts strongly with an Atlantic gannet, which is large, heavy, shorter-tailed and with a longer upper arm. Correspondingly the former can dive with great manoeuvrability into exceedingly shallow water whilst the latter can plunge deeply in turbulent seas. The total length of a sulid's wings does not always correlate with the bird's weight (see Chapter 1). Abbott's booby is lighter than the masked but has longer wings and a much longer upper-arm in relation to forearm, giving it a distinctive profile. And it has a much lower wing-loading. The female blue-foot, though no heavier than the masked booby, has longer wings. The Peruvian booby is heavier than the brown but its wings are comparatively short. Expressing the weight/wing-length relationship as a single index reveals a striking degree of species-separation due in large part to sexual dimorphism; the extreme smallness of the smallest male red-foot extends the range of the difference between this, the smallest species, and the heaviest, the Atlantic gannet. The latter's wing-loading is almost three times that of the red-footed booby. The red-foot has a long 'hand', useful in agile flying and superficial plunging, whereas the gannet's plunge is so heavy that a long hand would be subject to severe stress. Thus weight and wing characteristics are related to

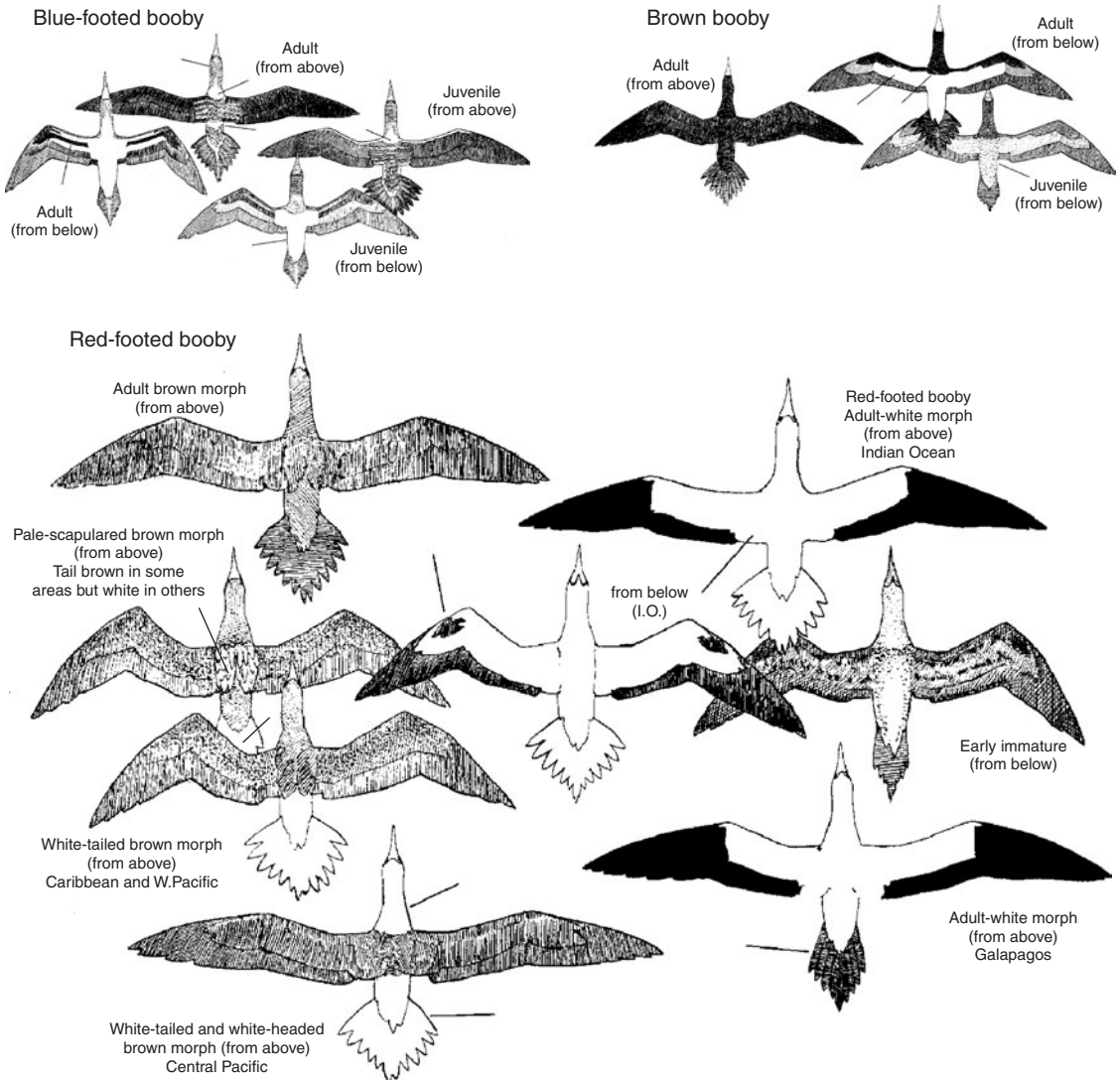
foraging behaviour and fishing techniques. It is more efficient for sulids with large foraging ranges in impoverished areas to have a high ratio of wing-span to weight compared with those in rich zones. And there must be significant differences in feeding niche between sympatric boobies as a consequence of morphological divergence, including unequal degrees of sex-dimorphism. However, light birds have light payloads and if, in addition, returns with food are comparatively infrequent, young grow slowly and

brood-size is minimal. These ecological features have become an adaptive and programmed component of breeding biology such that more food could not result in rapid growth or increased brood-size.

Ballance (1995) has calculated the energetic cost of flight in the red-foot, using doubly labelled water and activity recorders. The power required for flight (6 birds) averaged 19.0 ± 3.4 W (68.3 ± 12.1 kJh) which, significantly for the wider picture, was *less than one third* of the predicted value (62.1 W)



5.10 (a) External features of gannets/boobies. (Drawings: J.P. Busby.)



5.10 (b) External features of gannets/boobies (Drawings: J. P. Busby)

obtained from equations based on aerodynamic theory. Most of this difference was attributed to the red-footed booby's ability to soar, thus taking strong advantage of wind energy.

Sulid bills are fairly long, strong and pointed, but their shape varies widely between species and sexes. They are species-specific in cross-sectional profile and different in gripping power and functions such as speed of tip-movement, conferring different feeding capabilities. The upper mandible,

curved down at the tip but never hooked like a frigatebird's, is movable via the naso-frontal hinge, which helps to accommodate large prey. The bones of the lower mandible are incompletely fused in the region of the os spleniale and the special articulation of the quadrate permits an exceptionally wide gape from side to side. The cutting edges are serrated and there is a linear groove on each side of the culmen. In gannets, but not boobies, this is pigmented and forms conspicuous black

lines. The external nostrils are closed and openings at the sides of the base of the upper mandible are closed by movable, horny plates when the bird dives. In the gannet the palate is flat and ridged, the tongue small, the oesophagus extremely wide and dilated at the lower part, and the stomach small and thin-walled (Macgillivray 1852).

Binocular vision, important for three-dimensional appreciation, is provided by the forward-bearing eyes set close to the sides of the bill.

Bill, face, eyes and thick orbital ring are garishly coloured, imparting the clownish appearance which may be the origin of the name 'booby'. Pigments include melanin, eumelanin, phaeomelanin, carotenoids, and xanthophils which could produce the blacks, yellows, oranges, reds and presumably the greens and blues which occur. Red pigment can come from crustacean astaxanthin. Carotenoids and other pigments which cannot be manufactured must come from the bird's food. This could account for regional variation, which, however, is unlikely to have adaptive significance. Only in Abbott's booby do the sexes have completely different bill colours.

Sulid legs are stout and the totipalmate feet large. The tarsus is shorter than the foot with a reticulated surface continuing up from the toes as rows of small, scale-like scutes. In the arboreal red-footed booby the tarsi are shorter than in ground-nesters. The prehensile feet facilitate perching. The legs and feet are in some boobies startlingly coloured—tomato red in the red-foot, ultramarine in the blue-foot and lime green in the brown booby. In the gannets conspicuous yellow-green lines run up the toes and tarsi. These colours may enhance the signal value of the various flaunting movements used in display.

The claw of the middle toe, flanged and comb-like, is used to scratch the head and neck which are infested with feather lice.

Although sulids, like other pelecaniforms, lack a brood patch, they can incubate up to four eggs beneath their webs though the normal clutch is between one and three. The one-egg clutch is the derived condition.

Sulids hatch with just a few tracts of neossophtes and then develop thick, and usually long, white down. Abbott's down is noticeably scrubby—quite

different from the others—and differently structured. The down which eventually underlies the true feathers is not continuous with the chick down and does not develop from the same follicles (Witherby *et al.* 1940).

Locomotion

Like tropicbirds, sulids can remain continuously at sea. They swim buoyantly, tails clear of the water and neck partly retracted. Sulids fly powerfully, often alternating steady, fairly shallow wing-beats with glides, sometimes low over the surface, then lifting, descending or bearing away on a different tack. The slow wing-recovery between beats is due to the small pectoralis minor muscles, which raise the wing. Slope-soaring, using wave-slope dynamic soaring like albatrosses, and soaring in standing waves, are also employed. Some sulids, especially Abbott's booby, fly at great height when returning from foraging. Although extremely—sometimes ludicrously—reluctant to fly overland they will sometimes cross narrow necks. They land on water in a shallow dive rather than shooting their webs forward and skating along the surface like a pelican or cormorant.

Except for the two tree-nesters, sulids walk and hop well, almost always with closed or partly-raised wings and rarely holding them out for balance like a pelican, though they beat them when climbing a steep slope or bridging a gap. The tree-nesters and the brown booby perch adeptly, red-feet, in particular, perching comfortably in ship's rigging. Abbott's booby will launch itself suicidally across gaps in the canopy, landing heavily on the chosen branch.

Red-footed boobies regularly land in the colony after dark, even on moonless nights, but Atlantic gannets will not do so, preferring to sit on the sea until dawn. The others, too, are largely or entirely diurnal.

Body maintenance

All sulids have waterproof plumage, enabling prolonged periods at sea. It is maintained by the waxy secretion of the preen gland, transferred either from the bill or by rolling the head on it and then on the plumage (cf. cormorants and frigatebirds).



5.11 Australasian gannet taking off.

Jacob *et al.* (1997) have isolated a biologically active principle from the uropygial gland secretion of the Atlantic gannet which inhibits bacteria, yeast, moulds, and particularly dermatophytes.

All sulids scratch directly, that is, underwing, using the serrated middle claw; bathe, often in groups, with synchronous wing-thrashing, ducking and rolling and then rising and wing-flapping; wing-limber with leg-stretching and toe-clenching, one wing at a time, never upward wing-arching as in gulls and terns; stretch their necks forwards and upwards, or sometimes downwards, with depressed hyoid; fan their tails; head-shake from side to side; beat wings synchronously followed by rotation of head and neck and by a 'dogshake'; yawn sometimes with gross distension (lateral) of buccal cavity, and raise the upper mandible at the naso-frontal hinge. Adults sleep with head in scapulars, which they may raise so as almost to enclose the head. Usually they sleep standing up but often squat, especially if sick or exhausted, but they never lie prone with head on the ground, as chicks often do.

Body temperature is regulated by sleeking or erecting body feathers and by special behaviour. Reducing body temperature is often a problem in

the tropics and is achieved by panting and pulsating the bare gular skin, thus cooling the warm, moist air drawn over it. Sulids may excrete onto their webs, the resultant evaporation lowering body temperature. Closing the eyelids exposes more bare skin to the air and cloacal skin may be exposed by the appropriate posture. Besides erecting body feathers, some boobies (e.g. red-footed and masked) loosen their wings, cross the tips, and stand with their backs to the sun. Presumably this shades the webs and facilitates heat-loss but it may help to restore deformed flight feathers (see frigatebird Sunning). Red-footed boobies (though not Abbott's) save energy by hanging the head limply so that it dangles below the perch. Extreme heat conservation is rarely needed except by Atlantic gannets, where it is achieved by a combination of sub-cutaneous air-sacs, thick under-down, quilt-like body feathers and sub-cutaneous fat. The blood supply to the highly vascularized webs can be controlled so that, except when incubating or brooding, they are cold and do not lose heat to the environment.

Sulids drink seawater and excrete the salt via the nasal gland. Even when freshwater is available, they are not known to drink it.

Moult

Instead of all flight feathers being renewed in the same year, moult is semi-continuous though with pauses. It begins with the shedding of the juvenile innermost primary feather (generation one), in the gannet about six or seven months after fledging, and continues towards the outermost primary at the rate of about one feather per month (a flight feather probably takes about three or four weeks to grow). When the bird is a year old it has already replaced primaries 1 to (about) 6. Primary 7 of this new (second) generation is now growing while 8, 9, and 10 are still the original juvenile feathers. However, by now primary 1 is ready to be replaced again (by generation three). Thus three generations of primary feathers can coexist in the wing: the distal feathers still belong to the first generation, the middle ones to the second and the innermost to the third. This moult is described as continuous—staged—descendant. The secondaries moult in similar manner but the tail more irregularly and asymmetrically. Birds may grow up to six primaries at a time, three in each wing; usually only one or two are missing or partly grown at any one time. Wing moult is usually symmetrical (65% of cases in the Atlantic gannet). Because the cycles are staggered, adjacent primaries are never absent together and there are always at least two primaries between the nearest missing feathers.

Since it costs energy to grow feathers, moult is best undertaken when the bird is least stressed. Adult Atlantic gannets suspend moult around January to March (of 41 adults in early incubation none was growing feathers) not because winter is a hard time for them, but because they have by then (in Britain) returned to the colony and are undergoing their most stressful period—short days, long attendance stints, frequent display, and the flights to and from the colony. Replacement of secondaries and tail feathers starts from about laying time onwards and they resume primary moult just before the egg hatches when food is plentiful. Body moult becomes most apparent around hatching time in late May; feathers lie in deep drifts. Once moult has been resumed, it continues until at least November or December—again an easy time of year.

Dorward (1962) examined moult in detail in the masked booby. As in the gannet, primary moult began when the juvenile was 5–7 months old. At about 15 months when primaries 6 and 7 were growing, the innermost were shed again and a second cycle commenced although the first cycle did not reach the outermost until the bird was about 18 months old, at which time juvenile primary 10 was shed. Once the second generation of replacement began, the rate appeared to slow down to about one feather in almost two months, or not much more than half the gannet's rate, a difference which presumably reflects the booby's less plentiful food. There was time for a pause of only about two months in the year. As in the gannet, moult stops prior to egg-laying. Naturally, if suspension of moult is linked to the pre-laying period rather than to the point already reached in moult, and if laying varies from year to year according to environmental conditions, it is not to be expected that a bird could reach exactly the same position in the moult sequence for many years in succession. Successive cycles in adults were two or three feathers apart whereas in juveniles successive cycles were more spaced, the 7th



5.12 Sunning (wings spread) and energy saving (head hanging) in the red-footed booby. (From Nelson 1978b, drawing: J.P. Busby.)

primary usually growing before the next cycle began with shedding of primary 1. The above pattern is not invariable and the same primary, if injured, may be grown twice within a few months.

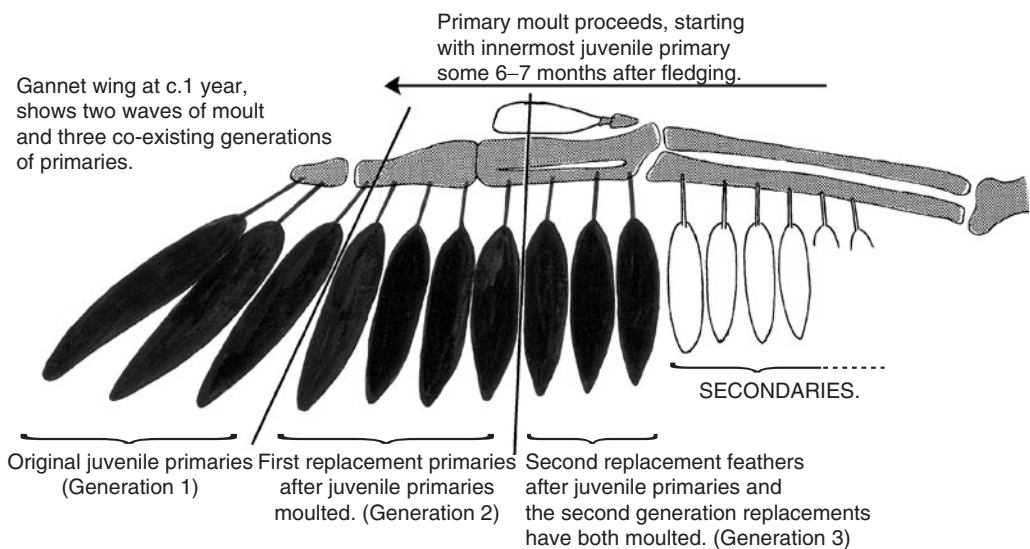
Abbott's booby has an unusual breeding cycle and its moulting pattern is not well documented. Of 15 adults accidentally grounded (March, May, June, July and October) 11 were in primary moult with one to three primaries per wing in growth (Sp Acc). A free-flying juvenile examined in May, two months before independence (≈ 10 months after hatching) had already moulted its innermost primary on each wing and was growing replacements. Moulded adult primaries were commonly found beneath nest trees only between August and December, when most chicks hatch, and shed feathers peaked four to six weeks after the main period of hatching.

Sulids in comparatively a-seasonal environments do not moult in synchrony—that is, the moult pattern of adults caught in the breeding colony on the same day do not resemble each other more than by chance. Nevertheless, the pattern is not entirely uniform from month to month, which indicates that external factors, probably those affecting laying (presumably food) do have some effect. Dorward showed that Ascension boobies tended not to moult in the peak pre- and immediate post-laying

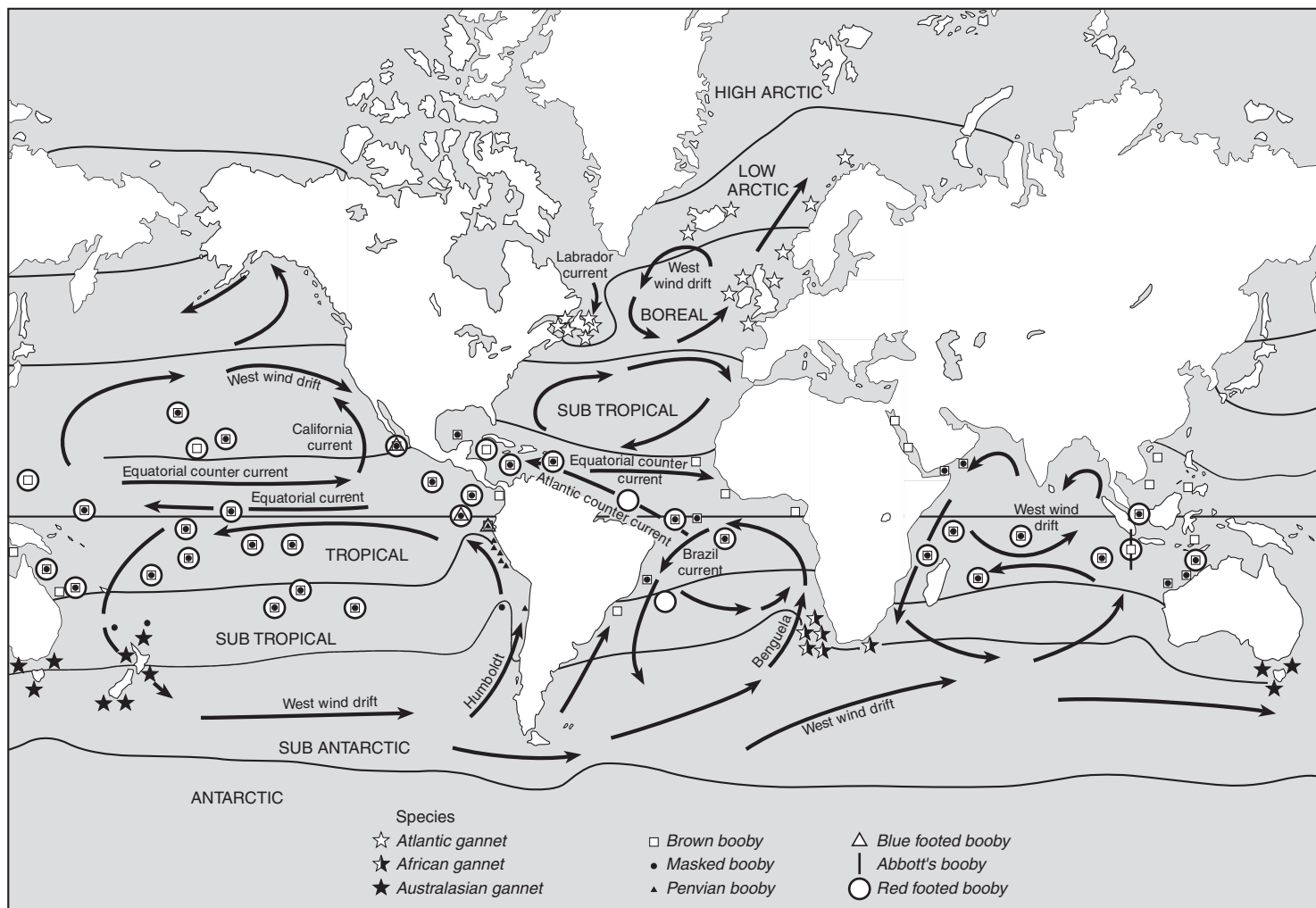
period. Then, as in all sulids, moult recommences when the young are well grown. In the Galapagos masked boobies suspended moult in the early stages of breeding but all birds caring for large young were moulting (Nelson 1967b).

Range and status

Sulids are widespread (Figure 5.14) and fairly numerous in temperate and tropical seas. One or another of the nine species breeds between $\approx 67^\circ\text{N}$ (Atlantic gannet) and $46^\circ 36'\text{S}$ (Australasian gannet) and across all three major oceans, a distribution equalled by no other seabird family of comparable size. Atlantic gannets in Newfoundland may find themselves incubating on icy ledges in blizzards of snow whilst on the equator the masked booby suffers extreme heat stress. However, only the three tropical boobies are widely distributed. The remaining species now have a restricted or highly restricted distribution; Abbott's is an endemic. Sulids are notably absent from the North Pacific. As Warheit (1990) comments, the Californian current off the central Californian coast is the only cold-water upwelling region in the world today in which there is no sulid. Yet they were present in the north Pacific as late as the Pleistocene.



5.13 Interrupted moult exemplified by the Atlantic gannet. (From Nelson 1978a.)



5.14 World distribution of gannets/boobies. (From Nelson 1978b.)

Possibly the Atlantic gannet breeds as far north as it can given its need for open water for a long season, and as far south as its main prey-species in the breeding season. It is the only *sulid* in its cold, stormy northern regions presumably because the ecological circumstances of these areas suit its particular combination of weight, bill strength, deep diving and far-foraging. This hypothesis is less convincing when applied to the other gannets. Both the African and Australasian have crossed into each other's breeding range and inter-bred (Sp Acc).

The Peruvian booby's dependence on the superabundance of its special prey *Anchoveta engraulis* in the Humboldt current region to which it has become adapted, presumably limits its distribution. The blue-footed booby impressed Murphy as 'falling between two stools'. Why is it so restricted and discontinuous in distribution? It appears substantially to have avoided competition with the three tropical boobies although it does overlap with all of them in places, even nesting cheek by jowl with the two ground-nesters. It seems only partially adapted to a true blue-water regime, even though essentially tropical. It may require the proximity of cool water and is locked into the narrow belt of seas west of the Americas, with an outpost in the Galapagos, but barred from extension westwards by vast blue-water belts, to the north perhaps by temperature, to the east by the isthmus and beyond it the equatorial Atlantic. Only by crossing the isthmus, which strangely it does not, could it reach the Benguela, with cool waters in a warm area which apparently suits it. There it would have to compete for nesting space with hordes of other seabirds.

The three sympatric pan-tropical boobies often share the same warm-water areas by using different nesting and feeding niches. The morphological divergence which underpins their differing ecologies includes highly unequal degrees of sexual dimorphism. Nevertheless they overlap considerably in the food taken. Although there are many locally enriched areas, such as the Arabian, Red and Coral seas, the Caribbean, Gulf of California, and around Revillagigedos and Tres Marias, which support large populations of two or all three species, the enrichment is generally low or medium. In evolving the adaptive syndrome which allows them to

exploit the large areas of only moderately productive blue-water, these three boobies may have forfeited the ability to penetrate the rich areas of the specialists. In fact, they are those *sulid* species which have adapted to the average features of the ocean-type which comprises the world's greatest area of bird-habitable sea. Flying fish is a staple of all three species and it may be that the upwelling off Arabia fails to attract warm-water boobies because flying fish are mainly absent (Bailey 1968). Again, the only areas where masked boobies penetrate further south than usual, off Peru, are where warm water does so.

The flexibility of most *sulids* makes it unlikely that, except in vast tracts of ocean containing few or no islands, the availability of nest-sites limits their distribution or numbers. Food apart, other possible determining factors such as insect pests (mosquitos apparently can cause seabirds to desert an island), climate, and natural predators are assumed to have comparatively little effect, though introduced cats, rats, and pigs can be catastrophic.

Commonly, three booby species occur on the same island, though rarely four (the Revillagigedos). Usually they prefer different habitats and never breed in truly mixed colonies though occasionally cheek-by-jowl at perimeters. That four *sulids* rarely breed together has no particular significance for, with the exception of Christmas Island (IO), there are extremely few islands which fall within the distribution of four species. The species-combinations which may occur on one small island are: brown, masked, and red-footed; brown, red-footed, Abbott's; brown, masked, red-footed and blue-footed; blue-footed and Peruvian; blue-footed, brown, and masked; blue-footed, red-footed and masked. No detailed investigation of such mixes has been carried out to determine the essential factors. Simplistically, species sharing an island prefer different nesting habitats and/or show distinctive foraging/feeding profiles. For example, red-footed boobies on Tower, Galapagos, nest in bushes or trees and feed offshore, sometimes at night, whilst masked boobies nest on the ground and feed offshore during the day. Such suggestions are unconvincing. Why, for example, should brown boobies be absent from the Galapagos? Figure 5.17 gives a

guesstimate of world populations, sharply down since I published *The Sulidae* (1978b).

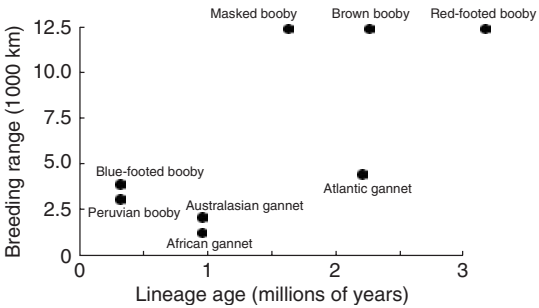
Movements

The four tropical boobies (red-footed, masked, brown, and Abbott's) may travel thousands of kilometres after breeding, resting on rocks and islands

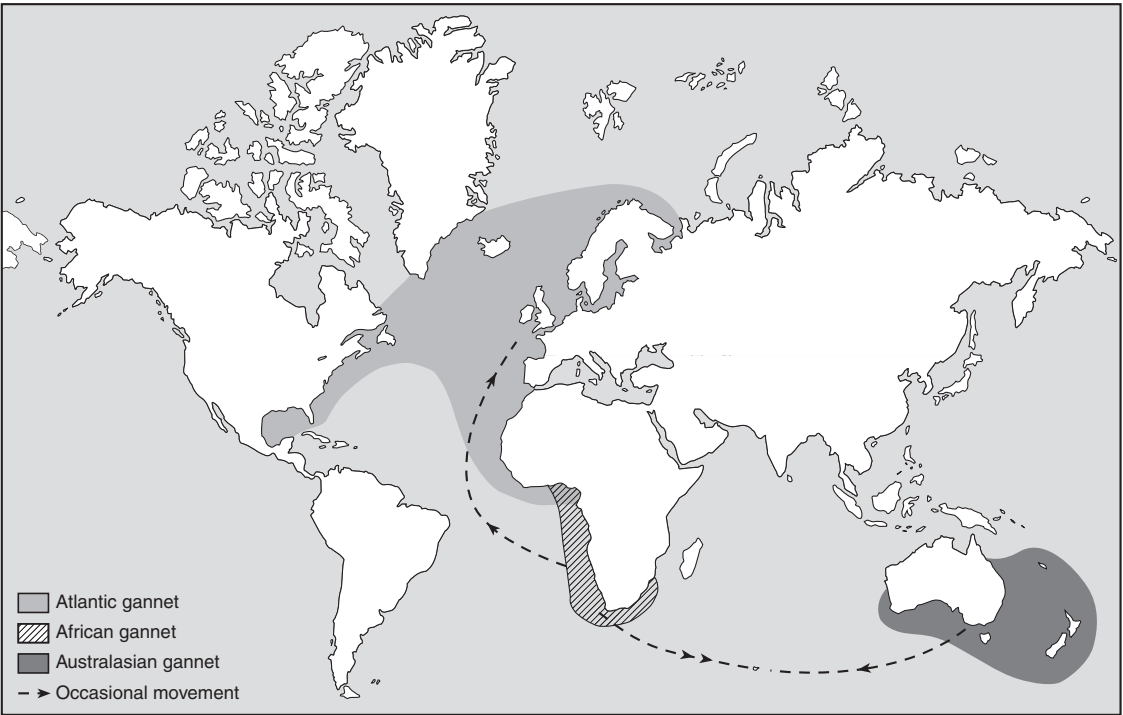
where they do not breed as well as at breeding localities other than their own. Many tropical stations are never fully deserted, although numbers may decline greatly from the seasonal high. Some individuals are always at some stage of breeding and those which are not may remain locally and (except Abbott's) even visit or attend nest-sites. In all sulids, juveniles tend to disperse or migrate further than adults. The main source of information on the movements of (particularly) red-footed and masked boobies stems from the POBSP ringing programme (Sp Acc).

Blue-footed and especially Peruvian boobies are more sedentary, generally remaining in the vicinity of the breeding area though they may emigrate during the unfavourable feeding conditions which attend ENSO.

The juveniles of all three gannets show true migration of between 3,000 and 5,000 km moving from colder and rougher to warmer and calmer waters. After return to home waters over a period of one to three years they do not again move either



5.15 Breeding range of gannets/boobies in relation to evolutionary age. (From Birt-Friesen and Anderson 1997.)



5.16 Distribution of the three gannet allo-species.

140 Pelicans, Cormorants and their relatives

5.17 Very approximate world populations (adult individuals) of gannets/boobies.

<i>Species</i>	<i>Probable upper limit</i>	<i>Possible lower limit</i>	<i>Comment</i>
Australasian gannet	150,000	145,000	Currently increasing in New Zealand and Australia. Many colonies last counted 1980/81. Most recent count (2000) awaiting analysis.
African gannet	350,000	280,000?	Confusing; apparent decline over decades but recent increases in South Africa, though Namibian population low.
Atlantic gannet	750,000	680,000	Currently increasing, both sides of North Atlantic. Rates of increase at individual colonies highly variable due to differential immigration.
Abbott's booby	5,000	2237 active pairs counted in 1991	Recent estimates: 2,300 pairs (Nelson 1978b); 2,500 pairs (Reville <i>et al</i> 1990a; Yorkston and Green 1992; Reville and Stokes 1994). Estimates highly reliable.
Red-footed booby	900,000	<600,000	Schreiber <i>et al</i> (1996) suggest <300,000 pairs. This, the most recent estimate, may be too low.
Masked booby	150,000	80,000	Population much declined and even the lower figure of 80,000 individuals may be too high.
Blue-footed booby	205,000	120,000	No reliable estimate; large areas with unknown population. Figures suggested here no more than a rough guide.
Peruvian booby	6,000,000	<3,000,000	Population fluctuates massively and estimates based on area and density open to considerable error. No recent figure.
Brown booby	500,000	<150,000	Population much declined and figure probably considerably nearer to the lower than to the upper limit. May even be below 150,000.

so far or so uni-directionally, reverting more to the sulid pattern of variable dispersion.

Unlike cormorants and pelicans, sulids do not travel overland except when storm-driven or, possibly, when crossing narrow land bridges.

Foraging and food

All sulids catch their prey by plunge-diving, adaptations to which include torpedo-shaped body, tapered bill, strong neck, cushioning air-sacs and binocular vision. Their lenses may have polarizing ability, since they are able to track underwater movements of fish in choppy water. They use partly opened wings, as well as webs, for propulsion underwater. All benefit from the ability to use the offshore zone, well beneath the surface; a feeding

niche closed to all potential competitors except the occasional tropicbird. The Peruvian booby is the one exception, since they limit themselves mainly to the inshore waters of the Humboldt, accessible, also, to the guanay, which can dive at least as deeply as the booby.

All sulids except Abbott's, will feed in the immediate vicinity of the colony, opportunistically, but their great advantage is that, unlike the cormorants, they can cover hundreds of kilometres in a single foraging trip. Blue-footed, brown, and Peruvian boobies show the strongest tendency to fish inshore whilst masked, red-footed, and Abbott's are more pelagic. Breeding blue-feet may be absent, presumed foraging, for less than an hour and red-feet for more than six days, but there is great variability within and between species. On



5.18 (a) Diving gannet. (b) The dive, just after entry. The old Celtic name for a gannet is derived from 'seth', an arrow. (Photos: A. & E. Bomford.)

average, an incubating sulid can expect to be relieved every one to two days, more frequently as hatching approaches and during early chick growth, then less frequently again.

All except Abbott's will feed communally, often diving in a dense hailstorm of criss-crossing groups. As has long been noted for gannets, the dazzling

plumage acts as a conspicuous signal, speedily attracting others. Concerted diving, far from being competitive, may enhance individual success by disorienting the prey and, under the constant barrage of diving birds, exhausting the fish's quick-swim mechanism, thus forcing it into the slow-swim mode. It is but a step from communal to truly cooperative fishing but it seems only the blue-footed booby has taken it (Sp Acc).

The white ventral surface found in all sulids except the brown morph of the red-footed booby may act as hunting camouflage since, against a light sky, it is less visible to fish and thus delays their avoiding action.

Like many other seabirds, boobies take advantage of fish driven to the surface by predators such as tuna and dolphins. The three booby species of the eastern, tropical Pacific often associate with marine turtles, particularly the olive Ridley *Lepidochelys olivacea*, which they use as a resting platform and to feed on fish that gather beneath them (Pitman 1993). Roosting on turtles may reduce the risk of predation by sharks. Ballance *et al.* (1997) found that 464 booby (red-footed and masked) 'flocks' in the eastern tropical Pacific (counting a flock as five or more birds including boobies as well as other seabirds) fed in ocean habitats which could be distinguished from those utilized by (mainly) sooty tern flocks or shearwater flocks. Booby flocks typically fed in areas in which the 20°C isotherm occurred at shallower depths (62.5 m) than in the case of the two other groups; and they had the highest chlorophyll content. In other words, they were the most productive patches. They suggest that two factors control the differences between terns, shearwaters, and boobies; energy constraints and competition. Sooty terns use less energy in flight than boobies and can afford to feed in waters of lower productivity. Shearwaters fall between boobies and terns in this respect. Competition will be highest in areas of high productivity and hence the boobies, being larger, win out.

Sulids are versatile feeders. They will plunge from a height of less than a metre to 30 or 40 metres at all angles from vertical or backwards of vertical down to 10 degrees to the horizontal, at high speed or slowly, powered by wing-beats or simply as a gravity plunge. Some species work surf-lines and

blue-feet, at least, commonly dive from the surface, submerging more or less on the spot with sharply inclined head and neck and a high flip of the wings, like a shag, or jumping almost clear before submerging. Juveniles swim with head submerged before flipping under, and this may be an important step in acquiring plunge-diving. Phylogenetically, plunge-diving, as a derived hunting method, presumably developed from the above type of feeding. Buoyant emergence may clear the surface and lead without interruption to a slanting dive. Sulids commonly feed in company with other seabirds, though booby, tern or petrel flocks are predominantly of one species (Ballance *et al.* 1997).

Kleptoparasitism

Persistent robbery of other species has not been recorded for any sulid, although opportunistic snatching does occur. On the other hand, boobies are regularly robbed by frigatebirds, though by flying high in groups 99% of red-feet can avoid attack (Le Corre and Jouventin 1997a).

Roosting, loafing and clubs

With the partial exception of Abbott's booby, sulids are notably gregarious, almost at all times. They roost and loaf communally, often fish communally and fly back to the colony in skeins.

Most roosts are on rocks, reefs or islands either near to breeders or otherwise. Assuming (perhaps wrongly) that none of the roosting or loafing individuals at breeding colonies are off-duty birds, such non-breeders, including adult-plumaged as well as immatures, may form a considerable part of the colony either on the fringes or among breeders (where they need to be taken into account when estimating the breeding population). Roosting and loafing birds characteristically rest, preen, and sleep. They may defend 'personal space' by threat, but do not engage in the other displays observed in gannet 'clubs'. However, the distinction may become blurred in boobies, because roosts may contain adults coming in to breeding condition and therefore likely to show incipient territorial and sexual behaviour. Roosts of boobies on islands where none

breed usually number scores or hundreds rather than thousands. Many are overnight visitors and may include foragers from a breeding colony. At such places, numbers may fluctuate massively throughout the year.

Clubs

In the three gannet 'species' all the behaviours used in breeding are performed, albeit usually at low intensity, in the gatherings of mainly immature plumaged birds either separate from the breeders, at their edges (often thousands) or sometimes in small groups, among them. These birds are confusable with pre-breeders. They may congregate far from any gannetry and be the precursor of a new colony, as in Iceland. A comparison of the composition and behaviour of such groups is needed. There are no fully equivalent gatherings among boobies.

Habitat and breeding biology

Habitat

Sulids are strictly marine, inshore through offshore over continental shelves to truly pelagic, and from foggy, icy, stormy seas off Newfoundland and Iceland to calm, clear, often impoverished, tropical seas.

Like cormorants and pelicans, sulids have adapted to a wide variety of nesting habitats on islands or, less commonly, on coastal headlands. The avoidance of land-masses is probably anti-predator; also the area inland is useless for feeding. But there are mainland colonies of Peruvian boobies, all three gannets, and masked boobies, and no doubt there were many more prior to man's impact.

Precipitous cliffs, flat island tops, craggy slopes, low bushes, and climax forest trees are all utilized. This adaptive radiation may reflect the intense competition for nesting habitat which, particularly in the evolutionary past, resulted from hundreds of millions of seabirds exploiting vast areas of ocean but compelled to share limited breeding space. Competition between ground-nesters presumably encouraged the ancestors of present-day arboreal sulids to take to trees and bushes. At present, masked, brown, and red-footed boobies are often sympatric and typically occupy different nesting

habitats (Sp Acc). There may be some overt competition between the ground-nesters—brown versus masked, masked versus blue-foot, blue-foot versus Peruvian. Abbott's booby, of ancient lineage, may have adopted its unusual breeding habitat (jungle canopy) when there were many more sulid competitors for ground-sites (see Chapter 1).

Colonies

All sulids breed in colonies though these range from a million or more densely-packed Peruvian boobies to Abbott's booby, whose single extant colony consists of well-dispersed breeding pairs. Colonies may be huge and dense, usually of one species only. Although red-footed boobies associate closely with great frigatebirds, sulids are much less likely than cormorants to nest among unrelated waterfowl. Sheer limitation of space often pitches sulids alongside other seabirds but these aggregations are never truly mixed.

Colony density may be more-or-less constant despite large differences in colony-size, as in the three gannets and the Peruvian booby or, as in all the other sulids, it may vary widely. Where, as in gannets, birds nest densely with little regard to available space, they are responding to social rather than topographical factors. Sites which, physically, are perfectly adequate may be ignored if they are too far from existing nests, whilst sites near to established pairs may be fiercely contested. Thus, on appropriate ground, an Atlantic gannetry creeps outwards whilst maintaining a more-or-less standard density, gradually blanketing the ground. Peruvian boobies behave similarly whereas masked, brown, and blue-footed boobies show more variable dispersion, responding to free space by spreading out. And they are more likely to nest in small enclaves or even solitarily. On Christmas Island (IO), for example, groups of brown boobies from two to more than a hundred pairs, at various densities, are scattered around the island's perimeter



5.19 Part of a colony of the Atlantic gannet; dense and even spacing of nests, synchronised breeding.

(Nelson 1972). Similarly, the density of red-footed boobies on Tower Island, Galapagos, varies enormously. Yet, of a thousand occupied trees, most seem to contain approximately the same number of nests at much the same spacing. Thus, whilst nesting density is variable, all sulids have a species-typical dispersion pattern whether in small groups or *en masse*.

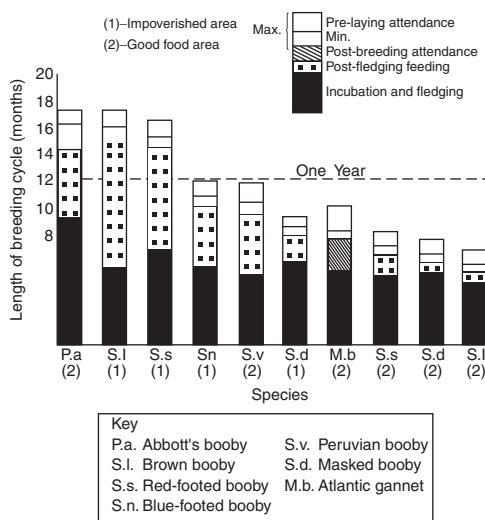
Frequency, timing, and duration of breeding

The pattern of attendance at the breeding colony varies with species and with locality. Where there are marked and predictable climatic changes which affect food resources sulids time their breeding to coincide with the optimal period and, usually, they breed annually. Where the climate is equable and food is either mainly constant or, alternatively, unpredictable, they breed non-seasonally and show, in some cases annual and in others non-annual cycles. Except for the Atlantic gannet the pre-laying and post-fledging periods of attendance are, in all sulids, about a month.

In strongly seasonal climes, photoperiodicity and temperature are the principal external variables

which trigger the individual's return to the colony, but in the tropics either endogenous cycles or the availability of food acting as a proximate timer (Nelson 1968) can trigger return and laying. The following are illustrations, taking in all cases successive, successful cycles and excluding replacement layings. Atlantic gannets, which inhabit strongly seasonal latitudes, show highly consistent mean laying dates and strictly annual cycles. Galapagos red-footed boobies, experiencing non-seasonal food, do not show consistent mean laying dates and waves of laying may occur at different times of year. And, because some pairs require more than a year for a complete breeding cycle, they breed non-annually. But elsewhere the red-footed booby may show approximately seasonal and consistently annual breeding, as on Christmas Island (IO). Yet the equally tropical blue-water masked booby, which is often sympatric with the red-foot, nowhere departs from an annual cycle although often it shows an extremely wide spread of laying. The tropical boobies that do depart from an annual cycle are Abbott's booby, some populations of the brown booby, and some blue-footed boobies. Abbott's booby breeds under a monsoonal regime (December–April) and lays mainly May–July, usually every other year since their cycle is too long to allow annual breeding. Ascension brown boobies may lay at eight–nine monthly intervals. In an a-seasonal environment in which food fluctuates irregularly rather than seasonally, the short, eight-month cycle increases the chances of coinciding with a favourable period. This advantage is increased if, over a long period (as apparently on Ascension) brown boobies remain ready to breed but lay only if food becomes favourable. The eight-month periodicity is thus flexible rather than, for instance, the mandatory nine-month cycle of the sooty tern. However, Ascension brown boobies may not produce young more often than conspecifics with an annual cycle as on Kure, or Christmas Island (IO) since they more frequently fail. Blue-footed boobies, similarly, may show a less-than-annual cycle (Galapagos) or an almost annual one (Gulf of California).

Clearly, therefore, the tropical sulids are flexible in the timing and frequency of breeding whereas



5.20 The composition of the breeding cycle in gannets/boobies. The gannet is the only species in which parents do not feed their offspring after these have fledged.

the seasonally constrained sulids are locked into comparatively inflexible regimes. That local populations of some sulids, rather than the entire species, have evidently evolved adaptive regimes which suit their particular circumstances implies substantial variability in the underlying physiology, but this remains to be investigated.

Unequal frequency of breeding means unequal lifetime productivity which, together with unequal brood-size, unequal success, and unequal adult mortality rates makes demographic predictions impracticably complex.

Territorial behaviour

Male sulids prospect for a site on the wing or perched, and then acquire and maintain it (both sexes) by overt fighting and/or ritualized display.

In dense-nesting sulids, notably the three gannets and the Peruvian booby, overt fighting is commoner than in spaced nesters. In the arboreal boobies where falling can be fatal, it is rare or absent. Even where sites are plentiful there can be fierce competition to acquire a socially adequate one. Fighting sulids use only the bill, never striking with feet or wings. All species possess ritualized threat, either in overt (bill-gaping) form or as territorial (site-ownership) displays. Many of the latter are complex but still readily recognizable as homologous within the family. Dispersed ground-nesters employ highly ritualized locomotion and then display at the boundaries with adjacent territories.

Like cormorants and pelicans, sulids can vary their facial expression and head-size to a remarkable degree by raising or sleeking all or part of the head feathers.

Aggressive behaviour in sulids may be related, in form, to the movements (and associated anatomy) used in catching fish; strong biting and rapid movements of head and bill. Vigorous and rapid jabbing, common between rivals in all sulids except Abbott's booby, may occur also between mates (masked, brown, blue-footed, Peruvian, and red-footed) but not in gannets, presumably because of its potential to release stronger aggression (Sp Acc).

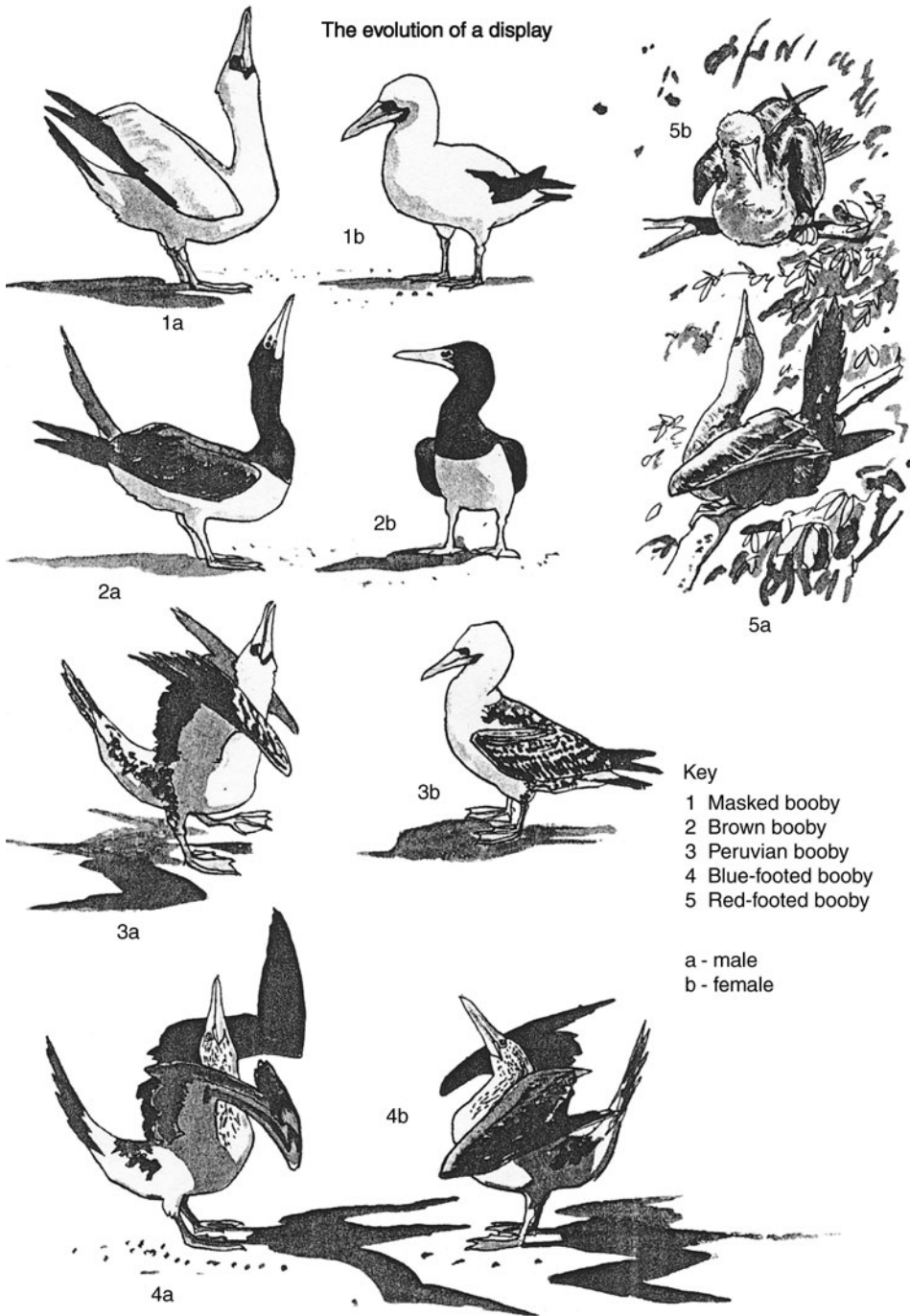
All site-ownership displays in the sulids incorporate or are interspersed with redirected aggression,

either touching or holding the substrate. But only in the gannets is it clear that the site-ownership display is actually derived from ground-biting. The functionally equivalent site-ownership displays of masked, Peruvian, and blue-footed boobies strongly resemble the food-begging of the juvenile. These three species strikingly illustrate how variation in the speed and amplitude of the same basic components can produce wholly species-distinctive displays. Thus the territorial display of the Peruvian booby looks quite different from that of the blue-foot simply by being slower, with movements of great amplitude.

Pair-formation

In five booby species (masked, brown, blue-footed, Peruvian, red-footed) the basic components of the male advertising display (skypointing—Figure 5.21) are the same and are probably homologous with the functionally equivalent display in cormorants (see Figures at the end of Chapter 5). In the gannets, by contrast, sexual advertising is extremely inconspicuous and not homologous with its counterpart in the boobies. Gannets possess the skypointing display but use it in a different context. Of the five boobies listed above, all except the masked employ skypointing both to attract a female and as a subsequent pair-bonding display (like cormorants). Only sulids which lack skypointing as a sexual-advertising display—gannets and Abbott's booby—have evolved a special and highly differentiated face-to-face greeting ceremony and, coincidentally or not, these are the only sulids with a lifelong pair-bond and the only ones to fall outwith the genus *Sula* (Chapter 1). A reunited pair of blue-footed boobies will 'advertise' (skypoint) repeatedly, and reciprocally, as a mutual display, whereas gannets and Abbott's booby perform their 'greeting ceremony'. In other words, the male blue-foot, when joined by his mate, simply re-enacts the display which initially attracted her, and she reciprocates using the same display, but the gannets and Abbott's booby do not use their 'advertising' as pair-bonding.

How may one interpret these differences within a closely knit family? First, by its close similarity in each of the 'core' boobies, the skypointing display



5.21 Sky-pointing in boobies. This striking display – sexual advertising and pair-bonding in function – is homologous in all these boobies, although each species has evolved its own distinctive version. (From: Nelson 1980, Drawing: J.P. Busby.)

confirms their relationship. Their common ancestor developed the precursor of modern skypointing and this display subsequently diverged in each of the derived species, whilst maintaining its basic form. This is especially clear in the blue-footed and Peruvian boobies, which are closely related and in which, correspondingly, skypointing is very similar in form.

The gannets, however, do not use skypointing for sexual advertising. Their's indicates their intention to move away from the site, in the context of change-over at the nest. Probably, in the ancestral sulid, skypointing was the signal of impending departure and the behaviour itself (neck-lengthening, bill-lifting, wing movements) derives from the intention movements of flight. If so, it is the boobies that have 'emancipated' the behaviour from its original function and the gannets that have retained it as a pre-flight signal. Gannets, therefore, have had to evolve their sexual advertising display from a different source. They have done so by modifying the display elicited by the approach of a conspecific—the site-ownership display.

Pair-bonding

Except for Abbott's, booby partners are mutually aggressive. Females appease by fleetingly turning aside the bill ('facing away'), most evident in the red-footed booby. Male gannets are conspicuously aggressive to females, especially initially, and females show extreme 'facing away'.

As sulid partners become accustomed to each other, the pair-bond strengthens, partly, in most boobies, via the sky-pointing display. But why skypointing (see Figure 5.21) should have become mutual and simultaneous in blue-footed and Peruvian boobies, reciprocal but not simultaneous in the red-foot, and unilateral, from male to female only, in the masked and brown booby, is unclear. The nuances of natural selection which bring about such changes are exceedingly difficult to interpret.

Ground-nesting sulids use many ritualized postures and movements which are exaggerated components of locomotion, such as parading with foot-flaunting and unusual head postures (Sp Acc). These protracted interactions follow flight-circuiting, sometimes with the partners in tandem, ending with a ritualized land-

ing which is particularly dramatic in the blue-foot. The partners thus become conditioned to accept each other's departures and returns, which is important in the early stages of pair-bonding. Although variously embellished or reduced in the different species, some form of flight-circuiting is common to all three core pelecaniform families, fulfilling both a territorial and a pair-bonding function. Its impact is increased by the loud vocalizations of the in-flying bird.

The arboreal sulids are largely debarred from locomotion-based interactions and there are notable differences between them. The red-footed booby appears to have a low internal threshold for aggression within the pair but nevertheless lacks a pair-bonding meeting ceremony. Its reciprocal skypointing is particularly prolonged and intense, possibly to subserve the bonding function. By contrast, Abbott's booby has an exceptionally high internal threshold for aggression. However, its greeting ceremony is, nevertheless, extremely highly developed (Figure 5.22).

In the three gannets, which are highly aggressive, there is much pair-bonding behaviour, including a well-developed greeting ceremony (see Figure 5.23).

Other sulid behaviour which helps to cement the pair-bond includes mutual preening though even such a simple activity varies within the family. Thus it is mutual (each preening the other at the same time) in gannets, masked booby, and Peruvian booby, but unilateral, mainly male preening female, in red-foot, blue-foot, and brown. In the red-foot it is scarcely sublimated aggression and, as also in the gannets, may grade into overt aggression in new pairs. Abbott's booby lacks it entirely, consistent with its lack of most other contact-interactions, seemingly relying on a high internal threshold to inhibit intra-pair aggression.

Mutual nest-building, whether the result is structurally functional or merely symbolic, provides further bonding.

Copulation (Figure 5.24)

Sulids mate at the nest-site (brown boobies may use a vantage point) and only the red-foot is recorded mating during darkness. Atlantic gannets, before egg laying, commonly copulate within 10 minutes of



5.22 The pair-bonding greeting behaviour of Abbott's booby; non-contact.

each reunion; twice in 5 minutes is common, with a maximum of 6 times in an hour. Before copulation, boobies perform ritualized behaviours (intention movements of flight or other locomotion). The red-foot lengthens its neck and wing-flicks; the Peruvian and blue-foot 'parade' (foot-raising); the masked approaches with conspicuously high steps. All booby females may stand or squat; Atlantic gannets do not stand but headshake violently. Receptive sulid females solicit by raising the tail and dilating the cloaca. Males mount either from the side or rear, boobies lay the bill alongside and 'nibble', but only gannets grip the female's head or nape. Treading, variable wing-spreading and waving and side-to-side tail movements prior to cloacal application are common to all males. The intense tactile stimuli of nape-biting and treading in the Atlantic gannet may coordinate the partners' behaviour, reinforce the pair-bond, and by sexually stimulating the female adaptively accommodate the male's otherwise disruptive aggression. The necessary tail-raising by the

female can be withheld to thwart insemination (only 70% of 506 brown booby copulations led to ejaculation) or she may fail to spasm the cloaca and defaecate copiously (Simmons 1967b). In the tree-nesters, mating is accompanied by a harsh grating call from the male red-foot and guttural clicks from male and female Abbott's booby, but vocalizations are not recorded for other boobies; gannets are silent. After mating, all sulid males tend to fetch nest material and this entails ritualized preparations.

Major variations within the family concern: the duration of the copulation period (range 2–12 weeks before laying, longest in gannets); time taken to mate (*c.* 24 secs gannets, *c.* 10 secs boobies); variation in form (only male gannets actually grip or bite the female's head); variation in frequency (up to several times an hour peaking in the week before laying). In the Atlantic gannet, copulation ceases with sight of the egg and restarts within 24 hours of loss irrespective of the degree of incubation, confirming that the male is inhibited by the egg.



5.23 The pair-bonding greeting behaviour of the Atlantic gannet; intense contact.

There is little information on extra-pair or reverse copulations. Simmons noted, for the brown, that of 84 birds already paired 20 males and 9 females were involved in extra-pair associations. Paired males tended to associate with unpaired females, and paired females mostly with paired males. In the blue-foot, extra-pair copulation occurred largely before peak copulation frequency; 7 females averaged 7, with neighbouring males, 7 males averaged 5 (Osorio-Beristain and Drummond 1998). I noted reverse copulations in the Peruvian, but not in the Atlantic gannet; blue-footed males and both sexes of Atlantic gannet attempted to mate with large young.

Nest (Figure 5.25)

All sulids except two ground-nesters (blue-footed and masked boobies) build structurally functional

nests, though the brown may build a substantial nest on cliffs or steep slopes but make do with a scrape on flat ground, though even here it will gather around itself a lot of material. Where other material is scarce, the Peruvian booby especially, and the African and Australasian gannets, build a nest of guano.

In the period just before egg-laying, nest-building activity is closely correlated with copulation and with the frequency and intensity of pair-interactions. This holds, also, for all other pelecaniform families except, possibly, tropicbirds. Males always collect most, or sometimes all, of the nest material but both sexes participate in building, even in those species with a merely symbolic nest. In addition to the basic nest-building movements common to all sulids there is a ritualized symbolic 'presentation' or 'showing' of nest material, swinging it in a wide arc with the bill pointing upwards, in the blue-footed, Peruvian, brown, and



5.24 Copulation, Australasian gannet. Note the exposed green gland (not an invariable feature).

Abbott's booby. It does not occur in the gannets. Why only some sulids have it is unclear. In all sulids the nest or site is an important focus for displacement activities during behavioural conflict. It is frequently touched, handled or even attacked. Such activities are 'punctuation marks' in on-going sequences of behaviour.

Egg/clutch

(See Chapter 2.) Sulid eggs are approximately elongate-oval, not markedly larger at one end. The comparatively thick, pale blue, green, white or pinkish shell has a rough calcareous coat which soon chips and stains. This roughness helps the webs to grip the egg during incubation. Smooth porcelain eggs which I substituted for gannet ones shot out from beneath the webs.

The most significant egg variable is mass, both absolute and as a proportion of female weight. All sulid eggs are small compared with those of most

seabirds, reflecting the altricial nature of the chick. At 100–124 g (7.1% of female weight but more in individual cases) Abbott's booby lays by far the heaviest egg (compare the Atlantic gannet's at 104.5 g or 3.3% of female weight). This difference is part of the adaptive web relating to the different growth-rates (via different feeding frequencies) of the two species. Obviously, each egg of polyparous boobies weighs less as a proportion of female weight than that of uniparous species, though the total mass of the clutch may be much greater.

Within a species, egg weight varies not only between individuals, partly in relation to age and experience of the female, but also between regions. The red-footed booby in the Galapagos lays a heavier egg than on Christmas Island (IO). The difference may relate to the greater likelihood that the hatchling will be forced to go longer without food in the Galapagos than on Christmas Island where food shortage is less likely. The value of the larger



5.25 Guano nest of African gannet. (Photo: J.P. Strijbos.)

single egg is thus plain, but in the case of polyparous sulids each hatchling is smaller than if there had been only one. However (excluding species which reduce their brood), the polyparous boobies live under ecological conditions which make the survival of more than one chick a reasonable prospect.

The three gannets, the red-footed booby, and Abbott's booby are invariably uniparous. The two latter are incapable of rearing more than one 'fit' fledgling although the Atlantic gannet can rear healthy twins (Sp Acc). The remainder of the family have retained the characteristic, common to cormorants and pelicans, of laying clutches of two or more. This larger clutch is an adaption to two quite opposite circumstances. In the tropical, impoverished-water masked and brown boobies the larger clutch does not enable the adults to rear two chicks but it does increase their chances of rearing one. But in the Peruvian booby, with usually reliable and

abundant food, the larger clutch maximizes brood size. In the blue-foot, the polyparous clutch plays both roles, allowing the adults to rear two or three young under favourable circumstances but hedging against lean times by incorporating a mechanism for brood-reduction.

Replacement laying

All sulids can replace egg(s) lost within the first half of the incubation period. Gannets will replace more than once, but this is not recorded for boobies, with the partial exception of the brown booby. Non-seasonal breeders are likely to be influenced by availability of food at the time.

Incubation (Figure 5.26)

Sulids incubate by applying their highly vascularized webs to the egg(s). The increased blood-flow



5.26 Incubation underfoot (Atlantic gannet).

through the feet, their tight application to the egg(s), the absence of a brood-patch and the matching of incubation behaviour to ambient temperature all indicate that heat really is transferred in this way. Thus the measurements which showed the internal egg temperature of the blue-footed booby to exceed that of the webs (Howell personal communication) must have been artefactual. In the red-footed booby the mean internal temperature of 11 adults was 36°C, and web temperature of 9 incubating adults 35.8°C, and of 10 adults with large chick 32.6°C (Howell and Bartholomew 1962). Tropical boobies spend much time with the eggs on top of the webs, where increased airflow and decreased contact help prevent overheating. Boobies may stand off incomplete clutches or even leave them unattended. Afterwards they may merely shade them. Retrieval of displaced eggs is poorly developed, though ground-nesting boobies (not Atlantic gannets) will sometimes roll those within beak-range. The position of the egg is frequently altered using the lower edge of the closed or slightly open bill. Only incubating gannets rise frequently and perform the site-ownership display, though all incubating sulids will preen etc.

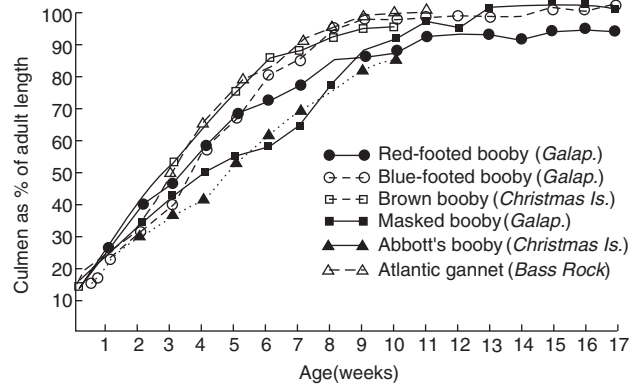
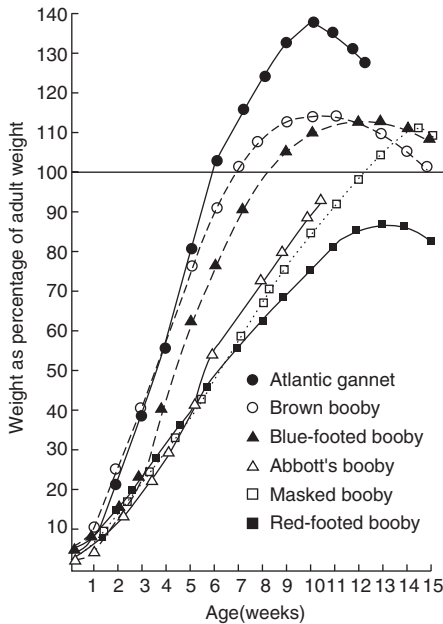
The sulids' incubation period of 42–55 days depending on species is considerably longer than that of cormorants and pelicans (28–35). Incubation period and the time taken for the chick to grow are positively correlated and, like clutch size, are adapted to ecological circumstances. Long incubation and slow development correlate with one-egg clutches and pelagic or offshore foraging, often in environments where food is, at best, patchy.

The sexes share incubation about equally with a tendency for males to take the first long stint. Stints vary with species, locality, and the stage of the breeding cycle. Pelagic species take longer stints than more-inshore feeders and within the same species, populations in impoverished zones take longer stints than those in food-rich areas. Stints shorten as hatching approaches. They are considerably longer than those of cormorants and slightly longer than pelicans'.

Although hatching chicks can emerge unaided, Atlantic gannets (and others?) may remove the shell from an emerging chick. Sulids do not systematically dispose of eggshells. Potential predators such as rats, cats, crabs, gulls, turkey vultures etc. are either there anyway, use cues other than eggshells, or cannot challenge an adult booby. Crypsis is thus unimportant. Throughout incubation, sulids regularly probe the nest bottom, and extract and fling away fragments, presumably removing hard objects which, because of point pressure, could puncture the egg.

Chick brood and brood reduction

All sulid chicks hatch essentially naked, with sparse white down which is similar in structure in all except Abbott's (Figure 6.60). Hatching skin colour varies with species and region, probably due to dietary differences. Down lengthens and thickens at species-specific rates. Again Abbott's is aberrant (Sp Acc) as it is, also, in developing a black cape of scapular and greater wing covert feathers and an unusual pattern of head feathers. Five sulids are uniparous; masked and brown boobies practise brood-reduction from clutches of two; only the Peruvian and closely related blue-footed boobies commonly rear broods of more than one chick.



5.27 Comparative growth in gannets/boobies. (From Nelson 1978b.)

Sulids illustrate (Figure 5.27) the wider phenomenon that the single chicks of pelagic species such as the red-foot and Abbott's grow more slowly than those of inshore feeders such as the blue-foot and Peruvian, even though the latter may have two or more chicks in a brood. The issue is made more complex by the marked influence of local features such as the proximity of food-rich upwellings.

Care of young

Newly hatched chicks would die if brooded beneath the webs. They are transferred to the upper surface, although the precise point in the period between the beginning of hatching and the emergence of the chick varies in different individuals, perhaps in relation to the adult's previous experience. In the Atlantic gannet, first-time breeders are more likely to delay transference and consequently crush the hatching egg. This inappropriate behaviour may be due to exaggerated latency—a slightly out-of-phase, delayed onset of

the adaptive response to vocalization and tactile stimuli given by the chick. It contributes to the lower success of first-time breeders. I have seen a gannet prise a dead, flattened chick from the bottom of the nest and place it correctly on top of its webs, though whether it was that individual that caused the death was not known. Boobies such as masked and blue-footed, which may nest on hot, bare ground, insulate chicks from the substrate by putting them on their webs or the chick may climb on.

Sulid chicks are brooded continuously for at least the first two weeks and then guarded for another two or three. They may then be left unguarded in boobies, more rarely in African and Australasian gannets and never, under normal circumstances, in the Atlantic gannet.

Even the newly hatched chick takes food directly from the adult's mouth, which can be difficult. Adults open their mandibles widely and engulf the chick's wobbling head, gently regurgitating a semi-digested bolus from which the chick can take fragments. The Atlantic gannet may bend

its head right over and lay the upper surface of the upper mandible onto the ground like a feeding trough. Sulids may stimulate small young by touching or gently grasping its head (cf. pelicans). In no case has an adult been seen to place food into the chick's mouth. Only in Abbott's booby is complete regurgitation of food onto the floor of the nest used as an additional feeding method when the chick is very small. Young masked and brown boobies scavenge accidentally dropped food with alacrity, whereas gannet chicks are reluctant; presumably the tropical species are hungrier. No sulid is known to bring water to its young.

At first, no sulid discriminates between its own chick(s) and others; all will accept foster young. But, at least in some species, discrimination appears later, when the mobility of the young makes intrusion possible (Sp Acc).

The role of reversed sexual dimorphism in the blue-foot is linked to chick care, the larger female contributing more than the male (Sp Acc).

Behaviour of young

Begging

The precise relationship between the amount of begging behaviour of the chick and the number of adult feeds has not been worked out for any species. However, it is clear from twinning experiments in the Atlantic gannet (Nelson 1964) that extra begging produces extra feeding, although whether this relationship is *pro rata* may depend on the age of the chick. In other words, twinned chicks fell slightly behind singletons at an early age, before the food available from the adult could possibly be limiting, which could imply an approximate pre-set quota of feeds to the very small young. However, once coordinated begging has developed, feeds more or less kept pace with demands and twinned young in some instances even exceeded singletons in weight. Obviously the availability of food to the parents is a factor, and where this is inadequate, as in artificially twinned red-footed boobies, no amount of begging can elicit sufficient food.



5.28 Restrained begging in two sulid species where energetic begging might lead to a fatal fall: A tree-nesting Abbott's booby B cliff-nesting Atlantic gannet.

All sulid begging involves bill-contact, head movements and stereotyped vocalizations. It reflects both the hunger of the chick and the nature of the nesting habitat. In all the boobies in which starvation is common, except Abbott's, frenzied wing-flailing and violent onslaughts on the parent are normal; but in Abbott's, even young in dire straits maintain restrained and highly ritualized begging, presumably as an anti-falling adaptation. Similarly, young Atlantic gannets beg in a restrained manner (Figure 5.28)—a trait found in some other cliff-nesters such as kittiwakes and black terns.

Resting, sleeping, and thermoregulation

Sulid chicks often rest or sleep whilst lying prone. After four or five weeks, unattended chicks of the

ground-nesting boobies spend much time standing, with head in scapulars. Possibly the unimpeded circulation of air over the webs facilitates heat loss. The red-footed booby chick makes a tripod by standing with its beak spiked into the nest bottom, tail raised and cloaca dilated. All sulids pant when heat-stressed and flutter the bare gular skin. Gannets excrete onto their webs and thus lose heat via evaporative cooling. Other sulids at least expose their webs which, whether by accident or not, are often excreta-soiled. Scapular feathers are precociously developed in all sulids and may assist in temperature regulation when the mean radiant temperature is above or below the bird's body temperature. To gain heat, all sulids shiver. All these methods are effective only when the chick has acquired reasonably thick down. Until then, brooding by the adult is essential. However equable the tropical environment may be, the micro-climates endured by ground-nesting boobies are often extreme; whilst even in more temperate latitudes sun, rain and cold can quickly kill young chicks. The constant temperature of 38–40°C maintained by newly hatched masked booby chicks, for example, is achieved solely by parental brooding (Bartholomew 1966) since small chicks have almost no ability to maintain body temperature above the ambient. By the age of three to four weeks, chicks can maintain normal body temperature when in shade. Shivering to produce heat appears at 10 days in masked boobies and soon becomes strong and sustained. Downy chicks shivered powerfully even with a body temperature of 38.5°C, which is in the lower range of body temperatures experienced during brooding. After around a month, chicks can reduce body temperature to about adult level but even newly hatched boobies will gular-flutter when mildly heat-stressed. Since a naked, overheated chick is mere minutes from death, it is adaptive to activate the cooling mechanism before any significant rise in body temperature.

Chicks distressed by hunger or temperature vocalize steadily, presumably to gain parental attention. Similarly, before hatching, pelican (and presumably sulid) chicks control adult incubation behaviour by vocalizing within the shell.

Sibling rivalry

The only sulid with broods of more than one in which there is neither siblicide nor competitive exclusion is the Peruvian, which usually enjoys super-abundant food.

Reactions to neighbours

Neighbours pose problems only in the more dispersed ground-nesting sulids in which the prolonged absence of foraging parents facilitates wandering by youngsters and intrusion by non-breeding adults. Sulid chicks are usually aggressive towards other young and even where an adult is on guard, chicks begin to threaten at about four weeks and soon develop adult-type ritualized threat. Masked boobies, with their large territories, invariably move several metres from the nest-site and tend to choose one spot as a resting-site. Chicks fiercely attack and evict strange young and, from about eight weeks of age, actively defend against intruding adults, by ritualized display, jabbing and wing-flailing. In response to attacks from other young or adults or in any alarming situation, masked booby chicks appease by tucking their bill. At first they do this even when moving alone around their territory. Similar appeasement behaviour is present in all young sulids except red-footed and brown boobies. In the Galapagos the lack of appeasement behaviour, combined with the tendency to counter-attack, sometimes cost red-footed booby chicks their lives when they were attacked by intruding, adult masked boobies. Brown booby chicks begin to wander at about 4–5 weeks and blue-foot chicks in the late stages of growth; parents may accompany them up to 20 m from the original site. In all three ground-nesting sulids, whose chicks are prone to wander, adults clearly discriminate in favour of their own young.

Young masked, brown, blue-footed, and Peruvian boobies show recognizable versions of ritualized territorial and sexual displays with accompanying vocalizations, even to overflying adults, as early as six weeks, which is long before juvenile plumage or adult size and stance have developed. Chicks of these species may interact with their parents in adult fashion and may in turn elicit sexual and territorial

responses from intruders. By contrast, young Atlantic gannets, red-footed, and Abbott's boobies do not behave in this way, possibly because of the associated danger of falling and the absence of an extended territory to defend against intruders. The adaptive significance of an extended territory in boobies may be to provide alternative resting places.

Crèching

No young sulids form crèches equivalent to those found in pelicans and some cormorants.

Fledging

Except for the Atlantic gannet and Abbott's booby, the basic family pattern is gradual attainment of full flight, following initial departure from the nest, wing-exercising and variably extensive wandering. However, the gannet's first flight has to carry it down to the sea, preferably well offshore, and in Abbott's booby must allow a safe circuit and return to the nesting tree; adults will feed their offspring only at the precise nest-site and any that fall to the jungle floor perish.

The fledging period ranges from 91 days (Atlantic gannet) to 6 months (Abbott's booby), consistently related to ecological circumstances (Sp Acc), especially the availability of food.

Post-fledging

All sulids except the three gannets continue to feed their free-flying offspring. Young boobies remain in the vicinity of the nest, on average for about a month, but up to six months in Abbott's and some red-foot populations (Nelson 1978b). Once they fly, young gannets are fully independent even though completely unpractised in feeding themselves and immediate post-fledging mortality is high.

Breeding success

Undisturbed sulids hatch 70–90% of eggs. Low hatching success is usually an artefact of disturbance or is due to abnormal climatic events such as ENSO. Failure can be due to behavioural incompatibility and parental inadequacy as, for example,

at change-over and during hatching, to infertility, perhaps affected by pollution, and to desertion. The latter can occur *en masse* in tropical boobies during severe food-shortage but is unknown in gannets; unfavourable feeding conditions cause extra-long foraging stints and hence unacceptably long incubation stints.

Fledging success varies much more than hatching success since starvation affects chicks more than eggs! Unguarded chicks are at risk of predation or conspecific interference. Consequently, fledging success varies between 20 and 90%, but is normally around 50–70%. The consistently highest success is in the three gannets and, in most years, the Peruvian booby. The lowest success occurs in those populations of tropical boobies which are most subject to food shortage. It is lowest of all in Abbott's booby, due to its especially disadvantageous ecological circumstances (Sp Acc).

In boobies, but not gannets, breeding success (reared to independence from eggs laid) must take into account the losses between fledging and parents ceasing to feed their free-flying offspring. In most sulids few fledglings die between acquiring full flight and eventually departing from the colony, but Abbott's booby's unusual regime means that in some years more than 80% of such fledglings die of starvation or from the effects of cyclones. Low productivity is normal in many seabirds and compensated by long breeding lives.

Three examples (Atlantic gannet, blue-footed, and Abbott's booby) illustrate intra-familial differences in productivity. A pair of adult gannets lives about 20 years, attempts to breed every year, has a brood size of 1, and a breeding success (fledged from laid) of around 70%. They thus produce 14 independent fledglings during their lifetime. Galapagos blue-feet live about 12 years, have a brood-size of 1.5, may attempt to breed every 9 or 10 months, and have a highly variable breeding success averaging about 40%. They thus produce 8.4 fledglings. An Abbott's booby lives 25 years, usually attempts to breed once every 2 years but takes some 'rest' years, has a brood size of 1 and a breeding success of around 30%. It produces perhaps 3 fledglings. Whilst all these sulids initially produce more than enough to maintain the population, even the

approximate figures given above indicate vastly different post-fledging (pre-breeding) mortality if one assumes a stable population. The young Atlantic gannet goes to sea on its own as soon as it leaves the nest. It lacks practice and any post-fledging support, and a high proportion of the independent fledglings die. Yet their population is increasing and, allowing for this, a pre-breeding mortality of around 78% is probable. A lower figure is to be expected for the blue-footed booby because the parents feed their free-flying offspring during the transition to independence and because blue-feet breed at a younger age than gannets. But even if the pre-breeding mortality rate were as high as that of the gannet, around 1.9 would survive. A pre-breeding mortality figure of around 70% seems likely. Abbott's booby has an exceptionally low productivity but the offspring that eventually depart have benefited from prolonged post-fledging feeding whilst (presumably) practising fishing, and therefore their pre-breeding mortality after leaving the island may be low, enabling the population to remain stable despite the unusually low productivity.

These examples, though imperfect, illustrate the huge variability in factors affecting demographic calculations in species with vastly different breeding regimes and the difficulty of reliable prediction.

Fidelity to colony, site and mate

Sulids that have once bred usually return thereafter to that locality, though not necessarily to the precise site. This breeding philopatry contrasts with the much less certain natal philopatry—returning to the colony of one's birth. Breeding philopatry ensures the continuance of sulid colonies which, unlike those of some opportunistic pelicans, do not disappear or spring up fully formed. Indeed, many sulid colonies are extremely ancient. The much weaker natal philopatry means that young birds may emigrate and either initiate new colonies or recruit into existing but non-natal ones.

Fidelity to a precise breeding site within a colony, although strong in some sulids such as gannets, is generally weaker than fidelity to the colony. With the probable exception of Abbott's booby, all

boobies are prone to move around locally, even though remaining faithful to the group itself. Site-fidelity is closely linked to mate-fidelity, since it enables partners to meet up for the new breeding attempt. Again, mate-fidelity is strong in gannets and probably in Abbott's booby, but the other boobies often change site and mate during their breeding lifetime.

Fidelity to site and mate is affected by the species' seasonality. In the tropics, breeding cycles tend to be other than strictly annual. They cannot be reliably geared to seasonal changes in light and temperature and may be much influenced by non-predictable variables such as food, presumably interacting with endogenous physiological cycles. Food flushes may act as triggers, and if the endogenous cycles of erstwhile mates have run out of phase (being non-annual) re-pairing may be impracticable. Consequently, partners may remain together for two or three successive breeding attempts and then diverge. The masked booby seems to be the only sulid other than the gannets with an annual breeding cycle throughout its range, and appears to show greater mate-fidelity than the other boobies except Abbott's, which, though a biennial breeder, is nonetheless seasonal.

Age of first breeding

Sulids take longer to begin breeding than any other pelecaniform except frigatebirds. They rarely breed until their third year, usually not until their fourth or fifth and sometimes even their seventh. However, species and regions vary. The most precocious booby is probably the Peruvian (highly favourable food resource), and Abbott's probably has the longest-deferred breeding. Gannets, particularly the Atlantic, have longer-deferred periods.

Deferred breeding in sulids is not related to body size. But it would be facile to try to relate it to the difficulty of the feeding technique since all sulids are plunge-divers and there is no objective way of comparing difficulty. In seabirds a relationship between offshore or pelagic foraging and longer-deferred breeding can plausibly be suggested (see Nelson 1990) and this could be important in sulids. Blue-footed, Peruvian, and brown

boobies are likely to breed earlier than masked and red-footed, and the two latter are the more pelagic. The Atlantic gannet seems, but may not be, anomalous. Its comparatively long pre-breeding period, despite inhabiting food-rich areas, could reflect the need to acquire local 'lore' and possibly its hunting of large, muscular prey in often stormy seas. Presumably this is more difficult than catching small shoaling fish in calm waters. Moreover, the adaptive web evolved by the Atlantic gannet requires the parents to provide more food, more quickly, than any other sulid, to enable its offspring to grow rapidly, evade seasonal constraints, and lay down extensive fat deposits to fuel the juvenile's unaided transition to independence. All boobies, by contrast, feed their fledged young.

Non-breeding years.

Probably all booby species (but not, or rarely, gannets) take 'rest' years in between breeding attempts. Thus there is always a proportion (probably highly variable) of non-breeding, adult-plumaged birds in a breeding colony. The dynamics of such individuals remain totally obscure. Interestingly, the only species which do not feed their fledged young (the three gannets) are also the ones which take fewest (if any) 'rest' years.

Longevity and mortality

There are too few direct and dependable records of annual adult mortality to make a full and accurate comparison, but sulids are clearly long-lived with considerable differences between species. Annual adult mortality ranges from a probable 3% or less in Abbott's booby, less than 5% in the Atlantic gannet, around 7% in the brown booby, and perhaps 10% in the blue-foot and Peruvian. These order of magnitude figures imply average life expectancy of between 12 and 30+ years with potential individual lifespans of at least 50 years and a proven one of 40 (Atlantic gannet; Nelson unpublished).

Causes of death

(See Chapter 4.) Natural losses occur through accidents at the colony: the arboreal red-foot

harassed by frigatebirds and, surprisingly, many gannets from awkward landings (broken or sprained wings), fighting and falling or being knocked off the cliff and striking rock. In 1974 Wanless recovered 120 dead or injured adults at the foot of Ailsa Craig; in 1975, 78 were recovered in just 4 months. Ailsa may be abnormal and an artificial factor might be suspected. 'Wrecks' of gannets are not recorded, though storm-driven birds occur far inland both in Britain and Europe; it is unlikely that many die at sea as a result of sustained stormy weather. They feed in near-gales and survive 2–3 weeks without food; adaptations to life in northern seas. They return fat from stormy winters at sea. But most mortality of juveniles in their first weeks is almost certainly due to bad weather sabotaging their first attempts to fish. Occasionally, wind from an unfavourable quarter (solan goose wind) occurs at peak fledging times and casts large numbers ashore. Other sulids may starve (during storms, ENSO), be killed by predators at sea (an unknown quantity) and (exceptionally) predators at the colony (Anderson 1991 suggests the Galapagos hawk may exclude red-feet from some islands). Parasite loads (which increase vulnerability to starvation) include: haemoparasites (brown boobies) (Work and Rameyer 1997), mites and ticks (*Acari*), nematodes, digenean trematodes and cestodes. Aspergillosis (a fungus) occurs. There are no records of epizootic disease causing large-scale mortality in any sulid.

Cormorants/shags

Introduction

Cormorants and shags form the most diverse and adaptable family within the Order. Twenty-nine species are marine, four fresh-water and six both marine and freshwater. Alone among pelecaniforms, they and the anhingids are adapted for underwater pursuit of prey by fast swimming. Although at home in a far greater range of habitats than any other seabird group, they are restricted to foraging comparatively near to the breeding colony and thus depend on predictable local food. Correspondingly, they produce broods of several chicks, which grow rapidly and soon reach breeding age, a

web of adaptations contrasting with those of tropical pelagic pelecaniforms. They are so proficient in their way of life that, presumably by competitive exclusion, there are usually no direct competitors from other seabird taxa. References cited in Species Accounts may not be repeated here.

Classification

Siegel-Causey (1988) summarizes all past attempts to classify the cormorants and shags, and on osteological characters proposes 2 sub-families, 9 genera and at least 35 species, compared with van Tets (1976) behavioural analysis of 2 genera and 34 species. I have retained *Phalacrocorax* for all, after Marchant and Higgins (1990) and del Hoyo *et al.* (1992), using 39 species.

The closest relatives of cormorants are the sulids, and then the pelicans (Chapter 1). There is good reason to demarcate the shags from the 'true' cormorants. Within the former, the complex group of allopatric, sub-Antarctic blue-eyed shags give the most taxonomic trouble. The anhingas and darters are treated as the single family Anhingidae rather than as part of the Phalacrocoracidae. For fossil cormorants see Chapter 1. For a history of scientific and vernacular names see Johnsgard (1993: Appendix 2).

The bird

Johnsgard (1993: Appendix 1) provides an identification key.

Voice

Away from the breeding colony cormorants are largely silent, apart from startled alarm calls and in some cases vocalizations when feeding communally, although no communicatory function is suggested. At the colony, guttural or raucous calls, and hissing, ticking, croaking, gargling, and almost inaudible puffing sounds are made, mostly by the male. Females are largely silent, or merely hiss. Probably, individuals recognize the calls of at least their mate and neighbours. Chicks utter rapid, high-pitched calls and in some species a most un-cormorant like

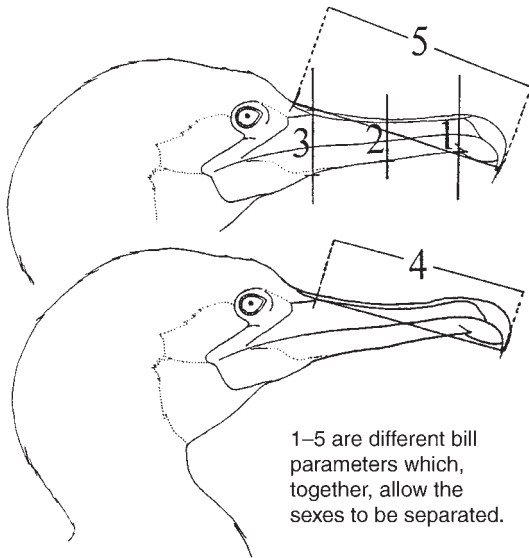
chirruping. Female chicks, in some species, begin to lose their voice at 5–6 weeks. Males retain their calls throughout.

External features and anatomy

Most cormorants are black, often with an iridescent sheen of metallic blue or green. On the back, greyer or browner feathers with black edges give a scaly appearance. Most southern-hemisphere species have white underparts whilst red-legged, spotted, and Pitt shags are grey. Juveniles are typically brown or dingy-pale, especially underneath. In all cases, the sexes have similar plumage, a feature of all pelecaniforms except frigatebirds (see Figure 5.29 for sexing).

Many cormorants display a nuptial adornment of filoplumes and crests. White filoplumes may be scattered over the head and neck or concentrated in conspicuous patches, as on the thighs of great, pelagic, and red-faced cormorants. Crests may be ragged or solidly recurved. Early in the breeding cycle a striking feature of the faces of cormorants, as also of boobies and pelicans, is the garishly coloured skin, eye, orbital ring, and sometimes the gape. Particularly in the blue-eyed shags there may be brightly coloured caruncles at the base of the upper mandible and papillae on the facial skin. These 'markers' may enhance display movements; soon after egg-laying the plumes are lost, caruncles or papillae shrink, and the brightly coloured facial skin together with the whole plumage becomes dull.

Black plumage may facilitate absorption of heat to compensate for heat-loss in a wet bird (Schreiber and Clapp 1987). However, in a cool climate black plumage loses heat through radiation faster than does white, which may be one reason why the blue-eyed shags of the Antarctic are so extensively white beneath. As in some sulids, some cormorants exhibit genuine colour morphs within the same population; some of the little pied cormorants of New Zealand have white underparts whilst others are dark. Intermediate plumages may occur where there are two colour morphs in the same population as they do, similarly, in the red-footed booby. In some cormorant species there are pronounced



5.29 Bill measurements allow highly dependable sexing of cormorants. (From Carss *et al.* 1997b.)

differences, between populations, in colour, though nothing is known about their adaptive significance.

Typically the bill is sharply hooked. The edges of the mandibles are not toothed but there is a nail at the tip of the hooked upper one (anhingids lack a recurved tip and have serrated mandibles; they spear their prey). In pelecaniforms the nasal glands lie in depressions within the orbit; cormorants have small ones but in the shags they are large and single-lobed, extending nearly the full length of the frontal bone (Siegel-Causey 1990). Some cormorant bills are grooved from the rudimentary nostrils to the tip, but although the secretion from the salt gland may run along them they are not essential; in cormorants, which lack external nostrils, the secretion drains into the palate and drops off the tip of the upper mandible. These grooves are not conspicuous in cormorants, as they are in gannets, where they may form 'sighting lines' when diving.

The sides of the mouth and throat are hugely distensible and the naso-frontal hinge can raise the upper mandible allowing cormorants to swallow large prey. The bone of the skull to which is attached the muscle which allows the bill to clamp onto prey is flexibly attached to the top of the skull

(the occipital crest). The supple neck is adapted for thrusting movements by the modification of certain neck bones (cervical vertebrae 7–9), a feature which reaches its extreme form in anhingids. The gular sac is used in heat regulation and in display, as in 'kink-throating'.

Features of the cormorant eye include the thickened and flattened cornea and the unusually well-developed muscles which regulate the size of the pupil and alter the shape of the lens, and thus the accommodation mechanism, underwater. The corneal features may minimize the effects of refraction.

The flexible webs and toes with claws facilitate perching in the tree-nesters. As in other pelecaniforms except tropicbirds, the claw of the third toe is serrated, presumably to rake out debris and feather lice. Pectinated claws occur in several terrestrial birds: barn owls comb their soft, light plumage; nightjars comb their rectal bristles and herons use one with talc to remove fish slime (Johnsgard 1993). In cormorants, and especially darters, Johnsgard suggests that the comb's teeth approximate to the spacing of the barbs on the breast feathers.

Skeletal features (which underlie the shape of body and wings) and the characteristics of the skull relate closely to foraging and feeding methods. Although these features are more conservative than plumage, and have been successfully used in comparative taxonomy, particularly by Siegel-Causey (1988) for cormorants and Warheit (1990) for sulids, it is still possible that convergent evolution is responsible for some resemblances.

Cormorant bodies are streamlined, somewhat flattened beneath. The neck is long. Unlike pelicans and sulids, in cormorants the furcula is not fused to the sternum. Such fusion, thought to be related to soaring ability, is found, for example, in frigatebirds and cranes (some cormorants, nevertheless, can soar beautifully). Cormorants, like pelicans, have comparatively broad sternums without the deep keel found in birds with powerful flight muscles (the pectoralis major and the supracoracoideus). In the double-crested cormorant, for example, these muscles average 12.6% of body weight or about half as much as in birds with strong flapping flight (Johnsgard 1993).

Cormorant wings are broad, long and fairly blunt; shape varies with species. Murphy (1936) noted that the guanay has exceptionally long wings associated with its extensive foraging flights in consistently strong winds. The Antarctic shags, to which the guanay is closely related, have broad, flat wings (batlike) and tend to stay close inshore. The length of the upper arm bone (humerus) in relation to the forearm (radio-ulna) significantly affects the shape and properties of a wing. In cormorants these are about equal in length which means that in general their wings are not of the high-aspect-ratio type found in albatrosses and also in pelicans, where the forearm is unusually long (see, for example, neotropic cormorant for wing-loading and aspect ratio).

Wing-loading is quite high, calculated as 1.00–1.08 g per cm² for the double-crested cormorant and 0.93 g for the neotropic, which compares with 0.74–0.84 g per cm² for anHINGIDS and 0.84 for the brown pelican (Hartman 1961; Owre 1967). The latter's buoyancy index, an alternative indication of wing loading, similarly indicates that cormorants are less buoyant than anHINGIDS or pelicans and by implication less efficient soarers. As inshore foragers cormorants do not need the high-aspect-ratio wings of typical pelagic foragers. Calculated figures (Hartman 1961) using an index derived from the relationship of wing length to width are: 2.68 neotropic cormorant and 2.86 double-crested compared with 3.9 for the brown pelican, whose wing aspect-ratio is almost as high as that of an albatross, the archetypal soarer, though the pelican's wing-loading is lower because its wings are broader.

No extremely small seabird which is still able to fly, for example the size of a storm petrel, could produce enough power to progress rapidly underwater by foot propulsion. Even the smallest cormorant, the pygmy, is 45–55 cm long and may weigh nearly 900 g. Male cormorants are usually larger than females and no species shows reversed sexual dimorphism. The flightless cormorant, at 4000 g, is, apart from pelicans, the heaviest member of the entire Order.

An important feature of any skeleton is its denseness, which affects the strength and weight of

the bones and thus the energetics of flight and the bird's buoyancy. Cormorant bones are much denser than pelicans' and vastly denser than those of frigatebirds but less dense than those of anHINGIDS, which are exceptionally 'sinkable' birds. The sturdiness of cormorant bones, for instance in the rib-cage, must help them to withstand the pressure of deep dives, which in some species may far exceed 100 m.

Like other diving birds, cormorants have a large volume of blood in proportion to total body weight, which helps to store oxygen for diving. Some species can remain submerged for three or four minutes, though this is eclipsed by the emperor penguin's 19 minutes and by the far longer submergence of seals which have special oxygen-storing compounds in their muscles (Schmidt-Nielsen 1975). Moreover, due to lack of fat, the intake of ballast, and the expulsion of air from the plumage, cormorants reduce their buoyancy. Since models of underwater locomotion (in ducks) indicate that more than a third of the work during descent, and even more during bottom foraging, is due to buoyancy, it is adaptive to minimize it (see Lovvorn and Jones 1991).

The legs are stout and set far back, and with the huge webs provide powerful stern propulsion. The marine shags, especially, have particularly long fourth toes, about 40% longer than the middle toe, which enhances the effectiveness of the thrust and is a feature of many diving birds. Walking and swimming depends on the anatomy of the pelvic girdle and legs. In the streamlined cormorant the former is about three times as long as broad whereas in the squatter pelicans it is only twice as long. Also, there are features of the pelvic girdle which facilitate powerful propulsion by the stout limbs and large webs. That part of the girdle posterior to the point at which the thigh bone articulates with it (the acetabulum) is appreciably longer than in pelicans. The associated muscles comprise about 10–12% of body weight in the neotropic cormorant, compared with 4.5–5.5% in the brown pelican. As for the leg itself, in cormorants the thigh-bone (femur) is considerably shorter than the shin (tibia-fibula) and distinctly bowed. The fibula, which is the thinner of the two shin bones, is

unusually well developed and in some individuals actually fused, with tibia which strengthens the limb for powerful thrusting.

Locomotion

Cormorants swim low in the water or partly submerged, tail awash and bill held slightly above the horizontal. On the surface they use webs alternately, but underwater kick with both feet together, adding a lateral twist. Before diving they may leap upwards, partly depending on how deeply they are about to dive, or they can slide under with scarcely a ripple. Underwater, they steer with their webs and tail but keep their wings wrapped around their lean bodies. Differences between sympatric species in diving and feeding habits are probably important in partitioning resources. An analysis of swimming movements is in Lovvorn (1990). On land they stand upright, with (when relaxed) retracted neck. They walk and hop with fair facility by comparison with grebes or divers. They may use outspread wings, like pelicans, to help them move uphill. Extreme cliff-nesters are unwilling to walk and the red-legged cormorant will usually fly rather than shuffle a few steps. Many cormorants are expert perchers and can balance on wires or rails as well as on twigs. Flight seems powerful, usually with continuous wing-beats. The neck is extended, in most species with head and body about in line though in some it is held, diver-like, lower than the body and with a downward dip at the base of the neck. On extended flights some cormorants retract their heads. Short flights are generally low over the water, but on passage cormorants may fly very high. Like pelicans and gannets, they often form V-shaped skeins. In sufficiently strong winds or cliff-side updraughts, they can soar and glide superbly. In level flight they can achieve 40 mph (60 kph). Like pelicans, they land on water feet first, depressing the tail as a brake. They take off from water, often laboriously, by beating heavily over the surface, kicking with both feet together.

Reduced buoyancy is important for speed underwater, and, as mentioned above, cormorants are helped by dense bones, lack of body fat, the shedding of trapped air from the wettable plumage

and even by swallowing small stones which are periodically regurgitated along with fish bones. They dive whilst breathing out (*contra* penguins), which presumably helps to reduce buoyancy.

Body maintenance

This comprises preening, oiling, scratching (foot under wing), yawning, distending the cheeks, raising the upper mandible, stretching, wing-limbering, panting, gular-fluttering, wing-shaking, body-shaking, bathing, and regurgitating pellets. Bathing is often communal and involves vigorous splashing and beating the water with the wings, rolling onto one side and head dipping. A bout of foraging is often followed by bathing and preening.

Melanin produces both the skin pigmentation and the predominantly dark plumage, but the metallic blue, green, or bronze gloss so characteristic of this group seems unexplained in terms of feather structure or physiology. Similar green, blue, or purple tones occur in the facial skin of cormorants and anhingids. Carotin is said to be entirely absent from these two groups although red may occur on the face, where it may be due to blood vessels beneath the skin. This, though, is unlikely to explain, for instance, the red legs and feet of the red-legged cormorant.

All cormorants apply the sebaceous secretion from the preen gland to their feathers, ostensibly to keep them flexible and waterproof. But are cormorants waterproof and if not does their habit of 'wing-spreading' serve to dry them? Cramp and Simmons (1977) state that they have waterproof plumage. Marchant and Higgins (1990) say of one of the southern ocean shags that 'small wings, heavy bones and water *permeable* plumage ... prevents long rests on water' (my emphasis). Hennemann (1984) says their plumage absorbs water but does not permit it to penetrate the layer of air next to the skin (yet cormorants seem unable to withstand repeated submergences for more than about half-an-hour). Obviously the outer plumage at least becomes very wet. Wilson and Wilson (1995) suggest that cormorants minimize heat loss by diving to greater depths when feathers are still dry and the air layer thickest, and birds with wet plumage minimize

energy expenditure by diving to shallower depths. Gremillet *et al.* (1998b) argue that cormorants control the volume of air in their plumage to minimize mechanical costs (upthrust) and thermo-regulatory costs.

After foraging, many species (including the vestigially winged flightless cormorant though not Antarctic or king shags or red-legged cormorants) seek a dry perch and hold out their wings facing the wind. Several different functions have been suggested: it dries the plumage; it indicates the presence of fish; it aids digestion; it serves to regulate body temperature; it balances the bird. A recent study based on the great cormorant (Sellers 1995) concludes unequivocally that it does dry the plumage and ultimately conserves energy. Thus it occurs only after a period of foraging when plumage is wet, birds face into the wind and spend longer in the wing-spread posture when wind is only light. They do it whether or not they have caught fish which destroys the digestion hypothesis. There is much variation in the time spent with spread wings but most of this depends on wind speed (assuming they dry more quickly in strong wind). It is inhibited by rain but sun has little if any effect on its duration. In about half the cases wing-spreading was accompanied by wing-flapping. The wing-drying thesis is supported by Lekuona (1999) for the great cormorant. Hennemann (1988) studied it in the double-crested cormorant and the anhinga and found that the cormorant showed the behaviour sparingly and without relation to ambient temperature or the intensity of sunlight. Anhingas spread their wings often, particularly at low ambient temperatures and in intense sun. Further, whereas the cormorant's metabolic rate does not fall at temperatures below thermoneutrality (thus not conserving energy), the anhingas metabolic rate did drop under these conditions. He thus concluded that the behaviour served different functions in these two species.

The signal 'I have been fishing' hypothesis refers to Jones (1978), who found that in the long-tailed cormorant it was strongly present in birds that had recently caught fish but absent in birds that had been equally long in the water but without success. However, Sellers points out several factors which could

vitiating this conclusion. Gremillet (1995) suggests that in the great cormorant it warms the stomach contents after eating cold fish. Captive birds always engaged in both wing-spreading and flapping when fed cold fish but did so on only 23% of occasions when fed warm fish. Concerning the mechanism, Meyers (1997) shows that in the double-crested cormorant the relevant muscles contain slow-twitch or slow-tonic muscle fibres which enable the posture to be maintained.

Moult

Cormorant moult is complex and the different terminologies used in authoritative accounts are often contradictory. Primary feathers are moulted in sequence from inner to outer but this is halted at intervals and taken up again later when, in addition, a new wave commences at a different point in the wing. This pattern, unusual in birds, is of disputed origin. Stresemann and Stresemann (1966) suggest that, as a consequence of interrupted moult in the first year, subsequent years involve two generations of feathers. Thus in the second year the outer primaries are older than the inner, though this does not explain why—i.e. for what adaptive reason—moult is interrupted. Cormorant moult starts, or resumes, or at any rate occurs mainly during late summer and autumn. In the juvenile European shag the primaries begin to be replaced about eight months after hatching, successive feathers being shed at intervals of about 17 days. Before the innermost primaries are a year old they are again replaced at about the time the first moulting cycle has reached the eighth juvenile primary. Both moulting loci then pause for the winter, when there is less time to feed. Successive primary moults begin each autumn and older birds will eventually end up with two, three, or even four generations of primary feathers in each wing (Cramp and Simmons 1977). This 'Staffelmause' moult better attunes energy requirements to the vagaries of food availability than would complete, seasonal, annual moult. The extreme opposite case is that of the anhingids, in which flight feathers are dropped simultaneously and the birds become flightless. Keijl and Symens (1993), for the Socotra

cormorant, note that between February and April most birds were in active moult (they breed September to March). The lowest proportion of moulting individuals was among juveniles and the highest among sub-adults and adults, 93% of which were moulting flight feathers. In these, 38% had two waves of moult and 11% had three or even four. In 52% two or three of the 20 secondary wing feathers were growing at a time but no juvenile had started secondary moult. In most birds, moult was asymmetrical. Tail moult appeared to be irregular but usually entailed a similar number of feathers on left and right. Unlike other cormorants, the Socotra appears to take less than a year for a complete moult, which could be due to feather wear caused by the unusually salty and therefore abrasive water of the gulf.

In most cormorants, moult has not been described in such detail (see Telfair and Morrison 1995 for analysis with particular reference to the neotropic cormorant; Hobson 1997 for the pelagic cormorant), but it is likely to be similar. The number of waves varies with species. Small ones, such as the pygmy cormorant, have only one or two. Two systems of tail moult, from or towards the centre, have been tentatively identified.

The body feathers of cormorants do not all emerge from the follicles that produced the chick's first downy plumage. There are apparently two generations of down (for instance chicks of the great cormorant grow a first coat of down beginning at around six days followed by a second during their second month). Second-generation down, if shed, is not replaced during pre-juvenile moult and its follicles may produce the downy under-feathers of the juvenile. Alternatively, the second generation chick down may itself persist. The contour feathers possess luxuriant down-like bases which, together with feathers called semi-plumes, provide insulation. The filoplumes, which are such a decorative feature of cormorant plumage early in the breeding cycle, are transient.

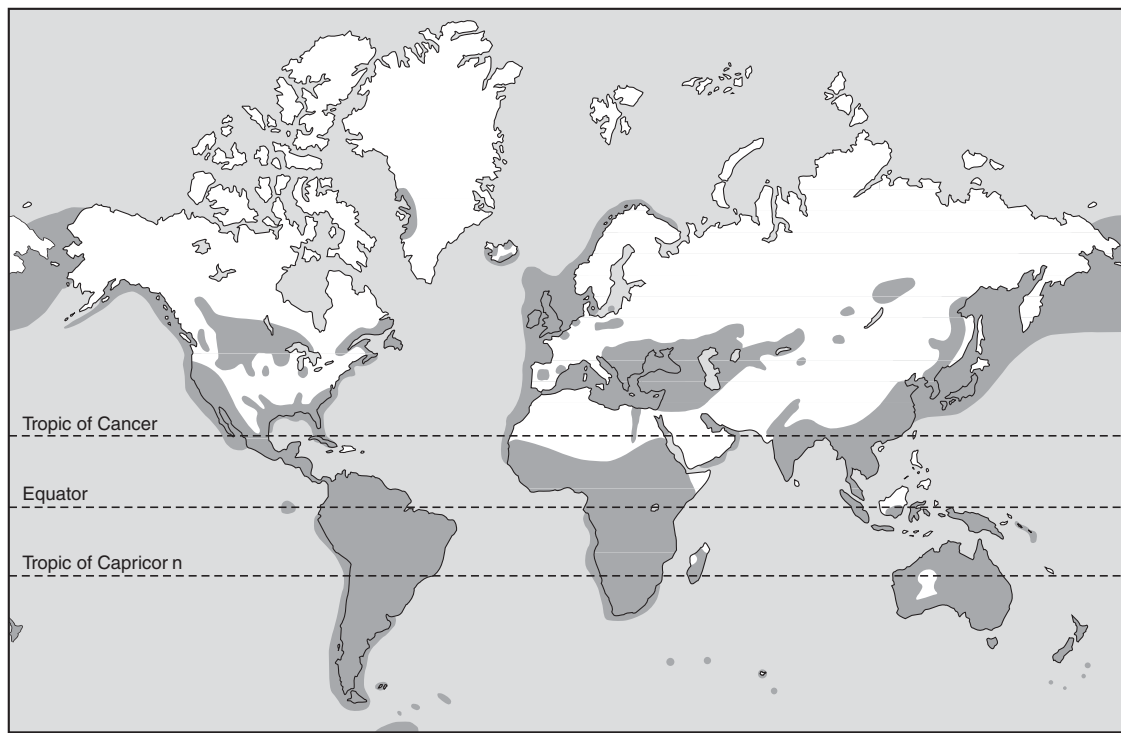
Range and status

Cormorants are widespread along most coastlines and on many continental inland waters. Marine

species are confined to inshore waters and although individuals occasionally make long sea-crossings most oceanic islands lack them. They are absent from north central Asia and from highly arid continental wastelands. They breed from well north of the Bering Strait south into the Antarctic, and around the globe. The greatest concentrations occur in unusually food-rich inshore waters such as the Humboldt, Benguela, and California current areas and in the productive waters of the cool temperate sub-Arctic and Antarctic regions, the latter associated with the Antarctic Convergence.

Van Tets (1976) suggests that the family's centre of origin is the Australasian region, which supports the greatest number of species. He speculates that several related cormorants early spread from this region across the southern oceans to the Americas. Another group, the cliff-nesting shags, spread around the edges of the Pacific to eastern Asia, western North America, western Europe, and North Africa. The large cormorants spread from Australia to Japan, South Africa and eventually, in the case of the great cormorant, across much of Eurasia and to the north east coast of North America. The great cormorant is the largest (though the flightless is heavier) and most cosmopolitan member, size presumably conferring advantage in surviving temporary starvation, including, during dispersal, coping with the widest range of prey size and in competing with other species.

Many cormorants breed in the same area or even in mixed colonies, with other phalacrocoracids and ibises, herons, and other water birds. But there is always a degree of niche separation achieved by differences in size and foraging behaviour and therefore in diet. In Argentina, red-legged, rock, and neotropic cormorants all breed in the Deseado estuary but in different niches (Albrieu and Navarro 1997). The least specialized species have the widest distributions, as in the great cormorant. By contrast, several of the Antarctic shags are endemic to specific, small islands and populations are extremely small. In between, the guanay and Cape cormorants are endemic to regions of high productivity whilst other species have patchy distributions presumably depending on particular



5.30 Approximate world distribution (not merely breeding) of cormorants and shags. (After del Hoyo *et al.* 1992.)

combinations of habitat factors, as in the cliff-dwelling shags. There are apparent anomalies such as Christmas Island (IO) with good nesting habitat but no cormorants. But since cormorants feed only in shallow water (or where inshore, upper-water-column fish are plentiful) the necessary characteristics may be absent.

Investigation of genomes in the great cormorant from 21 European populations (Goostrey *et al.* 1998), allowing separation of *P. c. carbo* and *P. c. sinensis*, showed that both forms were present, probably hybridizing, at sites in SE England.

Species population size varies from 700–800 pairs of the flightless cormorant to the tens of millions of the guanay. The world numbers of widespread species such as the great cormorant are impossible to compute. For example, a previously unrecorded colony of some 10,000 nests of this cormorant was discovered on Lake Victoria as recently as 1994 (Collins unpublished). See also Sp Acc.

Movements

After breeding, many cormorants disperse or migrate but most are not true migrants and some adults remain within the breeding area and may roost near the colony (Sp Acc). Because cormorants are not adapted to pelagic life they are unable to adopt the post-breeding marine nomadism characteristic of many seabirds and their young. Cormorants move along coasts or river systems, or over considerable stretches of land, including mountains. Not only are movements characteristically variable in direction and extent, but different populations of the same species may behave differently as, for example, in the great cormorant. Even within a population the pattern of movement in a particular year may depend on local feeding conditions at the time. This variability renders most generalizations at family level of little value.

The most sedentary species, endemic to particular islands or island groups, such as the sub-Antarctic and

Antarctic shags, remain around the coasts of their islands, apart from the occasional vagrancy, though there is local, post-breeding movement. Species such as the spotted and Antarctic shags, with wider distributions, may move further—up to 500 km in the spotted—or, as in some populations of Antarctic shags, move to more open water.

Inland, opportunistically breeding populations of several cormorants then disperse. Thus the great cormorant in Australia may breed in the wake of floods and then disperse rapidly and widely, even moving overseas, for example to Christmas Island, which lies 1,400 km NW of Australia (360 km S of Java). In Britain, juveniles and adults move in all directions, although in more northerly colonies such as the Orkneys the northward component is virtually absent. The S movement may take British birds as far as Portugal. W European cormorants *P. c. sinensis* are more strongly migratory than the nominate race, whilst in Africa they are largely sedentary.

The inland-breeding pied, little pied, and little black cormorants, and the black-faced cormorant, all of Australia, disperse to the coast or (little pied) even overseas if inland waters dry, though some populations may be sedentary (Marchant and Higgins 1990). After opportunistic breeding, the long-tailed cormorant of Africa moves away from large rivers when sandbanks become flooded.

In Europe the pygmy cormorant is both sedentary and migratory, wintering inland or on the coasts of, for instance, the Adriatic, Aegean, and Mediterranean. The autumn exodus from more northerly areas is triggered by falling temperatures.

In North America the double-crested cormorant may migrate from higher lakes to lowland waters. From late August, large flocks (10,000 recorded) from northern colonies follow the coastline in a southerly post-breeding migration, sometimes following river systems, especially the Mississippi. Often they migrate at low level but, as with some other cormorants, high-altitude movements (up to 1,000 m) may take place. Birds move north from winter quarters in late March, the migration gathering speed as it progresses. Non-breeders, presumably largely pre-breeders, may linger through the summer. Neotropical cormorants also move from

high to lower altitudes, gathering in thousands at inland and coastal locations.

Brandt's, too, show typical cormorant flexibility. At the Farallons, the largest colony in North America, some adults remain throughout the year whilst most go north and concentrate in central California (Ainley and Boekelheide 1990). Juveniles disperse mainly north but some go south. Similarly, the winter Farallon population of the dispersive pelagic cormorant varies from none to 100% of the breeding population. The most northerly populations of pelagic cormorants however, migrate consistently and do not return to their breeding colony until May or June.

Cormorants of productive upwelling areas such as the Humboldt and Benguela currents are compelled to move considerable distances only when food fails, as in ENSO, in which case millions of guanay and Cape cormorants, respectively, disperse widely, often in large flocks.

Eruptions in the European shag are well documented (Sp Acc). Movements vary between populations. For instance, due to local feeding conditions, shags from Lundy Isle, in SW Britain, vacate the island and move south across the channel and to Ireland, whereas those from the Farne Islands (NE England) and Bass Rock (SE Scotland) remain in substantial numbers at their breeding colonies. But even normally resident populations may erupt when food becomes scarce. All age groups then move further than usual. The extent and frequency of these movements seems to be independent of the size of the population. Many die, seemingly of starvation, or stress-induced disease. Norwegian populations of shags tend towards colony-specific wintering grounds (Galbraith *et al.* 1986), though these may change.

Foraging and food

Notwithstanding considerable adaptive radiation, all cormorants pursue prey underwater using foot propulsion (presumably the ancestral foraging habit). The pterodactyls, which had reduced wings, 'flew' underwater like penguins, and died out in the Miocene (Chapter 1). The only extant flightless cormorant (Galapagos) does not use its wings like that.

Cormorants are pelagic, estuarine/muddy-coastal and inland water species, though with much overlap. There is some partitioning of resources between species which feed in the same locality. Differences concern the part of the water column which is exploited (surface, mid, lower or bottom); the nature of the bottom which is typically fished over; the tendency to fish singly, communally, or even cooperatively; the use of aerial reconnaissance for fish-spotting and the foraging distance from base. Further, there is some evidence that where two species are similar in size and habit, their distribution is complementary rather than overlapping. Nevertheless, the following examples should not obscure the fact that often there is considerable overlap between species in the prey taken. In the cormorants of South Australia (great, little black, black-faced, pied, and little pied) the little pied is mainly freshwater, often using tiny pools. It includes crustacea and insects in its diet, dismembering the former by vigorous shaking in its strong, stubby bill. The similarly sized little black takes fewer crustacea and insects. It is slimmer with a slenderer, more sharply-hooked bill and eats a wide variety of small fish. The great cormorant feeds in various habitats and takes larger prey. To some extent, it may avoid competition with the pied by dispersing inland. On the Atlantic coast of North America, however, the great cormorant is marine, possibly minimizing competition with the double-crested, which occupies the inland-water niche (Van Tets 1976). Similarly in Britain, where it overlaps with the European shag (though not normally in the same colony), even when feeding in the same environment the shag took mainly sand-eels whereas the cormorant took none and had a more varied diet (Sp Acc). In the NE Pacific there are five cormorants (neotropic, double-crested, Brandt's, red-faced, and pelagic). In the east, the least marine species is the neotropic, which frequents protected bays and inland waters, including rivers, often at high altitude. In the north, the double-crested occupies most of these niches. Of the other three, which are entirely marine, Brandt's and the red-faced largely replace each other geographically, whilst the pelagic overlaps the ranges of both of these and pushes much further north, to well north of Bering Strait (Hobson 1997).

Double-crested and neotropic cormorants feed on mid-water fish, which often are in schools. Brandt's, pelagic, and red-faced cormorants feed more on solitary fish and invertebrates close to the bottom. Pelagics favour rocky reefs and Brandt's feed over both rocks and mud or sand. The pelagic has been netted at almost 60 m compared to the 1–9 m typical of most cormorants.

The little black often feeds in large flocks. Lines or circles of up to 100 or more swim abreast, sometimes with other species such as the pied. Double-crested have been seen feeding *en masse*, up to 2,000 in a flock, forming long, snaking lines of up to 50 or 60 close together. About a quarter of the birds are underwater at a time. Brandt's may form great rafts on the sea, although actual cooperation has not been described. Among the most spectacular feeding flocks of any seabird are those of the guanay cormorants of Peru. Like some other species—such as the great cormorant, the little black, and the red-legged—guanays reconnoitre from the air and its feeding flocks become huge. It feeds almost entirely on anchovies in the surface layer. Neotropic cormorants appear to fish cooperatively. Thus, within the family, communal, even if not cooperative, feeding is fairly common.

Wilson and Wilson (1988) compare the diving patterns of four sympatric cormorants (great, bank, Cape, and crowned). In the latter two species the deeper they had to dive and the longer they spent searching the seabed.

Most cormorant dives last considerably less than a minute and go no deeper than 10 m, but some species can dive deep and long. Imperial shags have been timed at more than four minutes (Wanless *et al.* 1992). However, foraging distance and diving pattern is flexible and, as in the European shag, may differ markedly in scarce and plentiful years. Species appear to differ in the nature of the correlation between time spent underwater and on the surface; some anticipate the time they will spend on the dive whilst others 'react' to the time they have spent (Lea *et al.* 1996, for great cormorant, European, pied, and little shags). Walton *et al.* (1998) show for the European shag that the ratio of dive-duration to time on surface is not depictable by a smooth curve; the relationship is more complex. Diving speed is about

0.69–1.01 m per sec (four marine species measured) and in underwater pursuit or search 0.34–1.45 m per sec depending on the feeding method and topography of the sea-bed. Closely adjacent colonies of imperial shags have been shown to use mutually exclusive foraging areas (Wanless and Harris 1993).

Besides swift pursuit of mid-water prey, great cormorants, for instance, feed extensively on fish concealed in mud or sand, using the tip of the bill to flush them. In exceptionally shallow water they may even hunt on foot. They may take eels to land before swallowing them bit by bit. Ducklings may be siezed from below, battered and swallowed.

Foraging distance varies with species and circumstances. Wanless *et al.* (1991) found that, typically, European shags from the May (E Scotland) foraged 7–10 km away, which is similar to some sub-Antarctic shags. Exceptionally, however, European shags will go several km further whilst guany cormorants may range perhaps 30 km or more from base. Cormorants cannot exploit dispersed food patches in largely impoverished offshore waters. They do not store food as body fat and cannot endure long fasts; they have to feed more frequently than, for example, the comparably sized gannet; cannot stay long in water and their flight is energy-intensive. Most members of the family inhabit cool, productive, inshore waters and are notably absent from tropical oceanic islands even if these support large numbers of other seabirds. Energy is saved by a physiological mechanism which allows cormorants to vary their body temperature by as much as 5°C, allowing it to drop when heat loss to the environment is high (as in water). They can increase their temperature using the sun (Wilson and Gremillet 1996). Because they do not stay long in water, feeding bouts in all cormorants, though variable, are fairly short. Cooper (1985b) found a significant difference between the foraging bouts of male bank cormorants (68 mins) and females (84 mins). The female is lighter, which may mean that she takes smaller prey and has to make more dives. During the non-breeding season, bouts were shorter. They spent *c.* 4 hours per day foraging, much as in other species. Presumably because they are larger, males dive deeper and spend longer submerged than females (Kato *et al.* 1999).

As in all skilled hunters such as raptors, terns, and the other pelecaniforms, the cormorant's preycatching takes time to develop. But from their very first dive there are inbuilt physiological responses such as immediate and substantial drop in heart beat (Enstipp *et al.* 1999). It has been noted that the dives of immature pelagic cormorants last slightly longer than the adult's, perhaps because they require more time to locate and capture prey (to be distinguished from the much shorter-than-adult's dives of newly fledged cormorants). Similarly, neotropic cormorants entering their first winter could dive as well as adults but were less successful (Duffy *et al.* 1986). Presumably, cormorants have to develop searching images and perhaps a range of hunting techniques.

Many species regurgitate mucous-covered pellets containing the hard parts of prey (otoliths, bones, crustacean parts, cephalopod beaks) together with small stones and grit. This trait has been used to determine their diet (see Russell *et al.* 1995 and especially Carss 1997). However, this method consistently underestimates the number and size of prey items and involves other sources of potential error (see Derby and Lovvorn 1997a; Suter and Morel 1996). Some otoliths are partly or entirely digested, especially from the smallest fish, leading to inaccuracies in determining fish-size and (if that is used to estimate weight) in daily food intake and energy requirements. Some otoliths in cormorant pellets may be from fish eaten by the cormorant's prey as Blackwell and Sinclair (1995) found for the double-crested cormorant. Casaux *et al.* (1995) assessed by feeding experiments the extent of otolith retention in captive imperial cormorants (*P. atriceps*). All except two fish species were under-represented, numerically, by their otoliths and one (*Notothenia rossii*) left none. Most otoliths were substantially eroded.

Chicks of the European shag (Scotland) began to produce pellets at 7–8 weeks at a mean interval of 3.7 days, but beads fed to them could take 5 days to be expelled, an interval at variance with several previous reports (Harris and Wanless 1991) (great cormorant Sp Acc). Despite the shortcomings of pellet analysis, they provide *c.* 90% of diagnostic fish remains against 10% from faeces (Johnson and Ross 1996). Daily intake is usually assessed from

pellet analysis and regurgitates, but Keller and Visser (1999) used DLW (doubly labelled water) technique to ascertain daily energy expenditure of great cormorants and calculated that they require to eat 539 g/day in the wild. However, the figure for daily food intake used to estimate loss to fishery interests may vary by a factor of 10 (Feltham and Davies 1997).

Conflicts between cormorants and fishery interests are intense (see great and double-crested) and large numbers are killed. One palliative, successfully used against double-crested, is repeated disturbance at winter roosts, which reduced their numbers on or near adjacent fish ponds by >70% (Mott and Boyd 1995; Mott *et al.* 1998). An aggressive and integrated frightening programme is essential. Schmidt (1998) describes barriers used against great cormorants in Bavaria.

Kleptoparasitism

Cormorants are more often victims than perpetrators of food-piracy, and whilst opportunistic snatching of prey from another individual occurs, kleptoparasitism is not significant in any cormorant.

Roosting, loafing, and clubs

Like pelicans, cormorants spend time, in some species amounting to 90%, in roosting and loafing. Cormorants loaf on cliffs, sea-rocks, inter-tidal reefs, island tops, beaches, sand-spits, ice, trees, bushes, reeds, and man-made artefacts such as breakwaters or even wires (neotropics, particularly agile, are able to sleep all night on heavily angled ship's stays); shags do not use wires. Daytime loafing and resting areas (there may be several for an individual) are used for preening and resting between feeding bouts; c. 8,000 long-tailed cormorants were recorded in dead trees after feeding. Birds may leave loafing areas and move direct to roosting areas (e.g. spotted shag). Nocturnal roosts are used for sleeping and may be traditional (e.g. great cormorant); probably most cormorants use several different roosts throughout the non-breeding period (mean 2.08, max 15, in the double-crested which may move nearly 400km between roosting areas, King 1996). In Spain 95% of

great cormorants stayed within 0–20 km radius; the mean distance between the roosting and feeding areas was 13.6 km and between nearest roosts 33 km (Lekuona and Campos 1998).

Cormorants usually gather at roosts some hours before dark and leave around sunrise. Guanays, at least, always return to roost on land, even after dark. Long-tailed cormorants arrive in small, high-flying parties and drop directly in to roost; others fly in by the thousand in skeins, on regular flight lines between feeding and roosting. Most species will share roosts and loafing areas with other species.

Often, a breeding colony is used as a roosting area, sometimes all year round. Breeding adults of some species, such as the Macquarie shag, may roost near the colony on the seaward edge and, at least in some species such as the king shag, roosts may develop into breeding colonies. Loafing and roosting groups are unstructured, usually consisting of loose groups within which there is no dominance hierarchy or, so far as known, preferential associations. As the breeding season approaches, some incipient courtship and territorial activity may occur in loafing areas. In the European shag, pair-formation commonly occurs on the sea-rocks away from the eventual nest-site, but there are no phalacrocoracid gatherings equivalent to the socially interacting but non-breeding aggregations or clubs found, for example, in some sulids and great skuas.

In some sub-Antarctic shags groups of immature birds—perhaps more than 100 strong—roost at the edges of breeding colonies, but immature and non-breeding Campbell shags are said to roost separately from nesting and courting birds. Towards the end of the breeding season young cormorants of many species roost near to the colony before dispersing more widely.

Habitat and breeding biology

Habitat

Of the 39 or so species, 29 are entirely or almost entirely marine; four (long-tailed, pygmy, Javanese, and Indian) are freshwater and six, especially the great, double-crested, and neotropic but also the pied, little pied, and little black, are at home on

the sea, in estuaries, and brackish water or inland. The anhingids are exclusively freshwater. Only, but importantly, the open oceans are barred to cormorants. They can feed in man-made ditches in the tropics and in the icy, stormy seas of the Antarctic. They can nest in jungle treetops and on the lowest, most barren and even spray-swept offshore rocks and on precipitous cliffs. Around 11 species can nest on flat ground; 9 on rocks, reefs and islets; 4 in caves or recesses on cliffs; 13 on cliff ledges; 6 on rocky slopes; 3 in reed beds; 11 in trees or bushes. Some use more than one habitat.

Colonies

(See Chapter 3.) All cormorants are colonial (Sp Acc) and characteristically mobile with respect to the location of the precise nest-site within the colony or sub-colony. By seabird standards and with a few notable exceptions, colonies are small. The factors which make pelagic seabirds aggregate in huge colonies (a vast feeding area but limited breeding locations) do not operate in cormorants. Their colonies are mainly of two kinds: the large, dense aggregations of the super-productive upwelling areas and the small groups of tens or hundreds, typical of many species, both inland and coastal (Sp Acc). Whilst some colonies, such as those of the sub-Antarctic island shags tend to persist, using the same locations on the island every year, as also does the European shag and others, some members of the family—for example the flightless cormorant, great cormorant, spotted shag, and others—change the location of the colony by a kilometre or more even if this remains within the same general area.

Like many colonial seabirds, cormorants may 'prospect'—that is spend time at a breeding colony in the year before they begin to breed. Schjorring *et al.* (1999) found evidence that such birds obtained high-quality sites and were more successful than those which had spent less time prospecting.

Frequency, timing, and duration of breeding

The enormous climatic variation within this family's global range imposes different seasons, durations,

and frequencies of breeding. In a-seasonal climates breeding may be almost continuous whereas in strongly seasonal ones it is confined to a short summer period. Cormorant breeding cycles, like those of pelicans, are very much shorter than those of boobies, tropicbirds, and (especially) frigatebirds. Like some pelicans, some cormorant species breed opportunistically, regardless of season.

The most variable component of the breeding cycle (from a few days to some months) is pre-laying attendance. Incubation varies between species only 24–32 days and the fledging period from five to about nine weeks. Post-fledging feeding typically lasts about a month but in some species and circumstances, several months. A representative cormorant breeding cycle occupies 19–20 weeks.

In seasonal climates and without regular exception, cormorants breed successfully no more than once a year. Among tropical species the flightless cormorant (female) can breed more often by abandoning the fledgling to the male's care whilst embarking on a new cycle with another partner. Otherwise, double-broodedness occasionally occurs in the bank cormorant, probably in the guanay and exceptionally in the European shag. In no cormorant is the length of an entire cycle too long for annual breeding. So-called rest years are not regular in any cormorant. This accords with their tendency to start breeding at a comparatively early age and to produce relatively large broods in a short period. However, some cormorants omit breeding under adverse climatic/feeding conditions, such as ENSO, and even in temperate regions the great cormorant and European shag, for example, may omit breeding if conditions are unfavourable. In such a year, a local breeding population may drop by a third, only to recover the following year. By contrast, genuine 'rest' years (as in frigatebirds and Abbott's booby) are independent of climate or food in a particular year and appear to be a means by which they avoid stress and thereby promote lifetime productivity.

Territorial behaviour

Cormorants reserve most of their extensive communicative behaviour for rivals and partners in the

colony. Elsewhere they express their motivation by avoidance or simple aggression. The Species Accounts show that each has evolved homologues of a number of ritualized breeding behaviours common to the family and in some cases homologous with sulid equivalents. The following comparison shows some of the similarities and differences.

Even where the colony remains in the same location there is little site-fidelity, though where there are durable pedestals, as in some Antarctic shags, pairs tend to retain them. Competitors are prone to usurp sites, even where breeding habitat is not limited. Cliff-nesters are most likely to encounter a shortage and in the pelagic cormorant territorial fights became more frequent after most of the extant nests had been occupied and as density increased (Siegel-Causey and Hunt 1981). On the other hand, the extreme cliff-nesting red-legged cormorant is unusually weakly aggressive in site-defence (Siegel-Causey 1987). Cormorant fighting or bill-grappling is brief and any face wounds superficial. Combatants may seize the opponent by the neck or wing or lock beaks and tug or push, often using a vigorous sideways head-shaking similar to that used to disable fish. They threaten by escalating from 'staring' and 'pointing' to 'gaping' and 'thrusting', sometimes with head-swaying (snaking) or rapid lateral head movements (tremoring). The neck is extended forwards and downwards and the head feathers raised. Males growl or bark raucously; females hiss and click. Although threat is commonest at the nest-site, birds may threaten as they move through neighbours or interact at the edge of the colony. During threat and pair interactions cormorants grasp nest material and make quivering or sideways-building movements ('nest-worrying' or 'nest-indicating') as re-directed aggression.

In a territorial display, the cliff-nesting rock shag flies in to its occupied site from below nest-level, uttering a rising call. Shortly before touch-down it back-flaps to reduce speed, bringing its pink webs right up, soles outwards. Elsewhere it omits this 'salute'. This, and a similar display in the cliff-nesting red-legged cormorant, resembles behaviour in the male blue-footed booby early in the pair relationship. These territorial behaviours occur even where there is ample unoccupied space.

Pair interactions

Usually, cormorants change partners for successive breeding attempts. Once the eggs have been laid, partners show little pair-bonding interaction, although during change-over, when landing at the site, approaching each other and departing, they perform highly ritualized behaviour.

The terminology surrounding cormorant sexual advertising, in which the male attracts the female, is confusing. Standard accounts, such as *The Birds of the Western Palearctic* (BWP) (Cramp and Simmons 1977) and *The Handbook of Australian and New Zealand Birds* (HANZB) (Marchant and Higgins 1990), both of which are based substantially on van Tets (1965), do not accord with each other or with other authoritative work, particularly that of Siegel-Causey (1986a, 1986b, 1987, 1988). To begin with a definition: Siegel-Causey's accounts separate 'male-advertising', which is a functional term for the display by which he elicits the initial approach of the female, from 'courtship', which is used to cover pair-interactions at the nest, including nest-relief. But 'courtship' should include pair-formation, whilst it is very doubtful that it should be used for 'recognition behaviour' and 'nest-relief'. 'Pair-interactions' is a better all-inclusive term which can then be subdivided into 'advertising', 'recognition behaviour', 'nest-relief' etc.

Second, one needs to decide what is 'a' display and what is merely a *component* of a display. This is essential when it comes to assessing homologues. An interaction usually involves many components which seem discrete when frozen in photos but are actually part of a mosaic whose overall message may depend on the frequency, intensity and position within the sequence of particular components. Sequences are variable. For example, an 'advertising' male may 'wing-flick' (which is one of the components) with or without 'throwback' (which is another). Or he may 'throwback' without the wing-flick, or do both with or without additional components, including vocalization. Yet in all these cases the composite display is 'advertising'. But two observers might seize on different parts of the whole and call *that* part 'advertising'. It then becomes impossible to understand different accounts.

Cormorants are particularly rich in sequence-behaviours. Their interactions may involve gaping, depressing the hyoid, stretching head and neck in various directions, raising head and neck feathers, 'clicking', nest-worrying and bowing.

Because of these points, and only for pair-interactions (a particularly good example of the evolution of variants in a homologous display), I include details which ordinarily would go in the Species Accounts. These will not be repeated elsewhere. Although there are too many unstudied species to permit a full comparative account, van Tets (1965, 1976) and Siegel-Causey (1986a, 1986b, 1987, 1988) have shown that many behaviours are homologous within the family. In a seminal reassessment of cormorant relationships based on the skeleton, the latter largely supports van Tets's classification based on plumage and behaviour, though his new classification is not universally accepted.

Pair-formation

I use the well-studied great cormorant and European shag (personal observations) as an introduction to pair-interactions in the group. Seminal work on the displays of the great cormorant is that of Kortlandt (1958, 1995, Archival, EGI), who made detailed observations on a Dutch colony in the days when field studies of courtship behaviour were extremely rare.

Male great cormorants advertise for a female, usually from an empty site. The folded wings are flicked rapidly up and down by a swivelling movement at the shoulder (see figures at the end of Chapter 5) whilst the head, crest partly raised, is retracted and the closed bill pointed upwards at about 45°. The spread tail is cocked vertically or towards the head. The body is horizontal with the rump up and the breast down. He remains silent, though his throat and cloaca pulsate in concert. After a variable period of wing-flicking without a break, and before the female has approached, he stops wing-flicking and performs the 'throwback', crown touching rump, whereupon his head rotates rapidly from side to side accompanied by a distinctive neighing vocalization (gargling), sometimes followed by a separate vocalization, 'goww, goww'. If the female *does* approach, the tempo of

throw-backing increases to about one every two seconds. After she has joined him he may throw-back repeatedly, interspersed with forward reaching with open bill and by nest-worrying. Sometimes males wing-flick, throwback and gargle and then return immediately to wing-flicking with, apparently, no female in the vicinity. A homologue of this display (see figures at the end of Chapter 5) is used by unmated males of all cormorants. It is thus important that the throwback and gargling is recognized as part of this sexual advertising display.

Confusion arises when the (false) impression is given, as in BWP and HANZB, that the throwback-with-gargling is *not* an integral part of advertising but, rather, is a separate display (variously called gaping, recognition or greeting).

Further complication arises through inconsistent use of the term 'gargling', which really refers to a sound rather than a movement, though (as in van Tets 1976) it is sometimes applied to an action. 'Gargling', meaning an action, is used synonymously *both* with sexual advertising, (in which case the user of the term intends to include the throwback component) *and* with the so-called recognition display. Indeed, in Marchant and Higgins (1990) gargling is used to mean sexual advertising in some species but recognition in others, which is not surprising since these two are basically the same display. Van Tets (1976) calls the throwback-with-the-gargling-sound 'gargling', and the same movement but without the sound he calls 'throwback', thus giving this *movement* two names according to whether it does, or does not, include a vocalization. This is confusing when comparing species. The female's 'gaping' ('recognition') is less complete than the male's, usually omitting the throwback before returning the head and neck. This is entirely consistent with 'recognition' being a reduced form of advertising.

Advertising in phalacrocoracids thus employs the throwback together with some head-rotating in the throwback position but, as is to be expected, the precise nature of the head-rotation ('head-rolling') differs in different species as does the throwback itself. In the Cape cormorant it is maintained for several minutes but *without* preceding wing-flicking. The tail is erected and fanned and the gular pouch distended. Upon the approach of

the female, the male extends his neck fully forwards. The male bank cormorant shoots his head forwards, then upwards and backwards until the bill is vertical, holds the position for a minute and then sweeps the head and neck forward and down. The throwback reveals and then covers the white rump, just as the great cormorant's wing flicking semaphores its white nuptial thigh patch. It may be that the great cormorant and some others, such as the double-crested and Brandt's cormorant, has added wing-flicking or equivalent in the context of advertising whereas some others have not done so, merely employing the (perhaps modified) recognition display for the function of advertising. This would not be surprising, since the approach of a potential partner for the first time (in response to advertising) and the approach of an actual partner thereafter (as in recognition at change-over) share much the same context and motivation.

Just as head rotation and throwback vary in form and duration between species, so too does wing-flicking. In the double-crested cormorant it is speeded up to vibration speed whilst in Brandt's the movement is described as a 'flutter' with wings quite widely spread. Fluttering may continue for half a minute at a time before the wings are repositioned and the head darted forwards and downwards, as many as 15 times. During this, the tail is cocked and spread, head and neck feathers ruffed and gular pouch distended. In response, the female may approach with elongated neck and assume a prone posture with head and neck horizontal and head feathers compressed—conspicuously different from the male. She may then jab at his head and adopt *his* posture, even proceeding to mount him. This close correspondence between male and female behaviour is characteristic of cormorants.

The pied cormorant's advertising conforms closely to the family pattern, the male wing-waving (equivalent to flicking) at a speed of one or two per second. Again, advertising grades into recognition, in which the head is swung backwards and forwards. As it moves backwards, and for the first part of the ensuing forward movement, the gular pouch is distended and the bill opened. Then, in the remainder of the forward movement there appears the familiar rotation of the head accompanied by

gargling with closed bill, except that here the rotation occurs with the head forwards rather than in the throwback position.

In the little pied cormorant the equivalent display is performed with raised crest and closed bill. The head may be swung in a vertical arc so far downwards (bill by now open) that it ends up below the feet, if the display is performed on a branch.

The European shag which, in essentials, resembles the other *Stictocorbus*, has conspicuous male advertising performed only during pair-formation. It begins with dart-gaping from a semi-horizontal position. Then the head is drawn back and repeatedly darted upwards and forwards whilst the bill opens to display the yellow gape. The tail is cocked and fanned. Then he lays his head along his back, points his closed bill upwards or backwards and jerks it without rolling or rotating. Head-darting may follow throwback instead of preceding it. Here, too, the distinction between advertising and recognition is not clear-cut. After the throwback the male may bring his head forward and down in a 'bow' through an arc of 180°. Females bow, too, but they don't 'throwback' and their bow is usually performed after gaping (see below). Male European shags may advertise on the sea-rocks where they dart-gape at females who come within range, rotating through as much as 100° to orientate display towards a moving female. The throwback occurs when the female approaches, which she does whilst performing the landing-gape (see below) at each hop, after which she maintains a sleeked, upright position for a few seconds. When close to the male she moves rapidly to a position beside and behind him, meanwhile throat-clicking. If she moves slowly, which many young females do, the male attacks her (Snow 1963), possibly because, during her final approach, the male performs the throwback but resumes the dart-gape just as she reaches him, bringing the two of them bill-to-bill, which elicits his aggression. If the female approaches quickly, the male is in the throwback or bow when she reaches him and their bills are not apposed. The female may then preen the male's head, which inhibits his aggression. After a few minutes she may hop away performing the landing gape with each hop, whereupon nearby males begin to dart-gape

at her. She may then visit one or more of them. This apparent choice process is found in almost all peleciforms during the earliest stages of pair-formation.

If the pair remain on the sea-rocks for some time the male may then lead her to the nest-site sometimes by flying—a possible source of the circuit-flying (pair flying round together and then returning to the site) common in cormorants, boobies and pelicans. If the distance is great, he may land at an intermediate point and display again, the female joining him, before moving onto the site proper. Snow's observations depict the crucial early stages in pair-formation. They illustrate the variability even in stereotyped behaviour under different conditions, for at most shag colonies display is mainly from the nest-site, with no 'leading-to-the-nest'.

The examples given above illustrate the complexity and yet the homologous nature of advertising; the throwback component is common to most cormorants.

Pair-bonding

An upward and forward waving of the head ('snaking' or sometimes 'pointing') is common between partners. The communicative role of the various head and neck movements widely employed, still need disentangling. In some species, display has become rigidly stereotyped; partners stand parallel and synchronize their forward stretching (See Fig. at end of ch. 5). In Brandt's, partners nibble and grasp each other's bill or gular pouch.

Cormorants have evolved highly ritualized versions of pre- and post-landing behaviour (Van Tets 1965). The ritualized hop seems universal. In the European shag the bird looks down at its feet and then hops. When landing from such a hop, or from flight, the bird gapes, exposing the yellow lining of its mouth, throws its head back, and holds its body upright with sleeked plumage. The bill is then slowly closed and the upright posture maintained for a second or two. The degree to which this posture is exaggerated depends on the internal condition of the bird; during early pair-formation it is more extreme than later. Shags gape when approaching their nest, or their fledged young, or even, in the

case of an unmated male, its own empty nest-site, with no shags nearby. It omits the gape when approaching a site which it does not own. During change-over the outgoing bird gapes, which, with the body posture, may signal impending departure. European shags lack an alarm call, and sudden flight without the posture might elicit panic departure by the mate, endangering eggs or small chicks. Immediately after landing, many cormorants enlarge the buccal cavity, imparting a distinctive discoidal appearance to the head. During movement on or near the site, they depress the tongue bone, greatly enlarging the gular pouch. This 'kink-throating', widespread in the family, is not so much a display with a discrete function as an adjunct to other displays, occurring in various situations such as courtship, pre-take-off, post-landing, and approaching the nest, during general interactions between partners and, in young birds, food begging. The pied cormorant accompanies kink-throating with a wide gape and a slow back-and-forth movement of the head in the recognition display. When a female approaches a displaying male she does so with kinked throat. The distension of the gular pouch in the pre-take-off posture is accompanied, in males of some species, by a ticking sound presumably equivalent to the throat-clicking of the European shag.

Partners on the nest-site often reach sinuously over each other's neck or back. Usually it is the standing bird which reaches over its sitting mate, lowering its hyoid bone and moving it up and down with the 'throat-click'. This occurs as pre- and post-copulation behaviour in the male and in both sexes as greeting and pair-bonding display. Sometimes, as in the European shag, the ubiquitous head-swaying occurs as an adjunct to throat-clicking. In several cormorants, partners throat-click from a position side-by-side.

Shags commonly 'point' and 'dart'. In pointing, the neck, head, and closed bill are stretched forwards and upwards with feathers of head and neck erected. In the context of recognition, in for instance the king and imperial shags (Siegel-Causey 1986a), it was always performed very deliberately by either sex on the nest. It was held for one or two seconds and followed by nest-worrying. In other

cases it was combined with darting, usually by the male. A shag darts by repeatedly retracting its head with forward-facing bill and then rapidly tremoring it from side to side before bringing it forward again. After several bouts of darting the male king and imperial shags point, thus starting a new cycle of point-darting. Point-darting is often performed by the male when alone on the site, often followed by ritualized preening of the white alar bar and breast feathers. As in all pelecaniforms, allo-preening is directed mostly to the sides of the partner's neck.

In sum, the widespread if not ubiquitous elements of behaviour during cormorant pair-interactions are: throwback in advertising-cum-partner-recognition; some form of wing-action (flicking, waving, fluttering); snaking; darting; gaping; forming a discoidal head; throat-kinking; throat-clicking; exaggerated post-landing and pre-departure postures. This extensive repertoire exists despite the relative impermanence of the pair-bond which, in some shags, may be broken not only between breeding seasons but during one.

Copulation

Usually, cormorants mate on the nest-site but sometimes on adjoining perches or even, double-crested, on water. Copulation begins three or four weeks before the first egg is laid but is most frequent (up to three times an hour) between 10 days before the first egg and 3 days after the second. The European shag may mate >100 times in a season. Female soliciting may involve ritualized behaviour such as, in the European shag, 'bowing' and 'gaping'. Long-tailed cormorants precede copulation by pecking each other's head, crest raised. Female king shags precede and follow copulation by facing the male, gaping and head-swaying and maybe nibbling the tip of his bill. In the European shag, mounting is accompanied by the landing-gape and vocalization. Before and after copulation, the great cormorant (both sexes) may point-gape, singly or mutually, and the female often handles nest material. They may preen each other (not simultaneously). Mating takes only five to seven seconds (though the male may spend longer on the female's back), may be accompanied by vocalization and involves a

single cloacal application. The female flightless cormorant worries nest material and continues to 'bow' during mating. Male European shags, and presumably others of the *Stictocarbo* group, grip and shake the female's neck, changing sides rapidly. The double-crested cormorant also grips. Cormorants which do not grip, such as the great and flightless, may 'nibble'. The great cormorant beats its wings loosely and tramples, though others may simply flex their wings. Post-copulation behaviour may include various ritualized elements. The male European shag dismounts with the landing gape; female great cormorants slowly and deliberately perform a forward stretch at 45°, a movement used, also, in other pair-interactions; allopreening and displacement activities directed towards the nest are common. In all pelecaniforms, nest-oriented behaviour is closely associated with sexual activity.

Reverse copulations seem common in at least some species, though Snow (1966) did not record them in the flightless cormorant.

Extra-pair copulations have been noted in the great cormorant (Kortlandt 1940) and European shag. In the latter it occurs mainly when a female responds to a male (other than her own) advertising from his nest. DNA fingerprinting revealed that up to 18% of chicks may result from a female mating with other than her mate (Graves *et al.* 1992, 1993b; Graves and Ortega-Ruano 1994). The frequency of extra-pair paternity was correlated with the level of reproductive success in the colony; pairs with smaller broods at fledging are more likely to have an 'extra-pair copulation' chick (Graves *et al.* 1993b).

Nest

In all cormorants the nest is structurally important, either to raise the contents above a sloping, stony or muddy substrate or provide a nesting platform on ledges or in trees. In the double-crested cormorant nests may be 2 m high and there is strong competition for persistent nests. In all cormorants the male gathers most of the material (sometimes from as far as 1 or 2 km), in some species before advertising for a mate but in others, such as the great cormorant, pilfering usually prevents this. In some, the female may bring it before the first egg

is laid. Copulation is usually followed by a trip for material, often gathered communally; dense groups of great cormorants congregate to pluck vegetation. In the flightless cormorant, gathering is accompanied by a courtship vocalization called 'growling', and by an incomplete version of courtship 'snake-necking', which corroborates the strong motivational connection between gathering nest-material and sexual activity. Where material is scarce the nest may be made of excreta, which is 'saved' and voided at the nest, as in the guanay cormorant (Hutchinson 1950). Nests of the Antarctic shag on South Sandwich were built entirely of penguins' tail feathers. Except for the flightless cormorant, which may swim on or beneath the surface whilst carrying material, all cormorants either fly or walk with it. As with some sulids, courting males may make token trips for symbolic scraps before returning with the ritualized accompaniments. Touching, handling, and quivering (sideways head movements which insert the material into the structure) are frequent adjuncts to courtship. Even where the building movements are functionless they still persist. Often, partners hold the same piece of material.

In most species the male appears to choose the nest-site. Either he leads the female to it, or attracts her by advertising from it, in which case she chooses site-plus-male. But in the flightless cormorant either sex may lead. The peak of building occurs well before laying begins and there is considerable variation in the interval between completion of the nest and laying. In the European shag the normal interval is three days but it may be much longer. This variability, as also that of the intervals between successive eggs, is presumably adaptive by delaying breeding during temporary food shortages.

Egg/clutch

Cormorant eggs, ovate-elliptical, are plain, pale blue, or green, covered with a chalky deposit which soon stains. Individual eggs never exceed 3–4% of female weight, though a large clutch can represent 12–13%. Egg-mass varies with sequence-position within the clutch, studied particularly in the South Georgian shag (q.v.). Egg-mass and the interval

between successive eggs are significant adaptations because the former affects hatchling weight, and the degree of asynchrony between hatchlings affects their subsequent growth and survival. In general, first and second eggs are roughly equal in size and in the chance of producing a fledgling, whereas third eggs are smaller and less successful. Cormorant clutches, most commonly three, frequently four, and sometimes five, are large for a seabird. Single-egg clutches are not typical of any cormorant.

Replacement laying

Clutches lost early in incubation may be replaced (Sp Acc).

Incubation

No cormorant incubates eggs beneath its webs. Instead, the webs are inserted beneath the eggs, which receive warmth mainly through the feathers of the abdomen. Powell *et al.* (1996) demonstrated the importance of periodic egg-turning; over 70% of eggs of the double-crested cormorant, manually rotated once a day, hatched successfully against only 54% unrotated. Incubation stints are rarely more than 6 hours. Both sexes incubate but in some species the male takes the bigger share. There is no 'egg-neglect', that is, deliberate and normal vacation of the nest and eggs, to permit the partners to forage simultaneously. Neglect would be impracticable where pilfering and predation is common. But the first and second eggs are not intensively incubated before the clutch is complete; the intervals between the hatching of eggs 1, 2 and 3 are less than the comparable ones between their laying dates. There is some evidence that incubation behaviour improves with age, reflected in the shorter incubation periods of older females.

During nest-relief, cormorants perform several of the courtship displays—such as the landing gape, ritualized hop, kink-throat, throat-clicking, snaking, pointing, and darting—but this declines as incubation proceeds. No cormorant has an elaborate and prolonged greeting ceremony like that of some sulids. Usually the incomer is largely unresponsive and change-over is quick. Because there are several change-overs per day, there is less egg-loss in the

early stages than in pelagic species with long stints, since such females may already have endured a long pre-laying stint and may desert if the male is slow to take over.

Cormorants do not systematically remove eggshells, which often lie near the nest, although they may be mandibulated and dropped over the edge.

The incubation period, range of means 28–32 days, is short compared with other pelecaniforms, except pelicans. It correlates with rapid development of the chicks and inshore feeding. The short incubation stints (1–7 hours is fairly typical, see Sp Acc) reflect the short-range foraging.

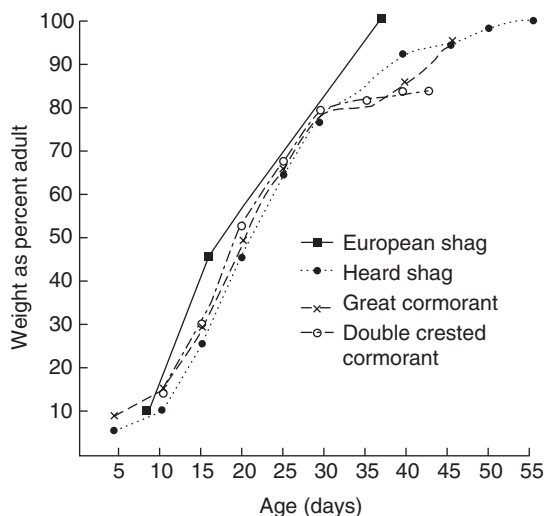
Chick, brood, and brood reduction

Chicks hatch naked and helpless with eyes closed. Skin colour varies with species, from grey to blackish. The first down (protoptile) is sparse and varies from almost black, through grey-black, fuscous to whitish on neck and (in some) underparts. Succeeding, dark, down (mesoptile) is thicker and woolly, though the head and part of the neck are often bareish. The first generation of feathers are usually clear of down after 40–50 days. Chicks grow rapidly (Figures 3.16 and 5.31). Brood size, usually 2 or 3, varies between 1 and 4. Unlike some boobies, no cormorant practises obligative brood-reduction in the sense of inexorable sibling-murder, but Hunt and Evans (1997) point out that in the double-crested cormorant 4-egg clutches never give rise to 4-chick broods. In that broader sense these authors employ the term 'obligate', but the reduction is simply by competitive exclusion from food. As in the comparable sulids and pelicans, the extra egg(s) act as insurance. In broods of fewer than 4 all may survive. In favourable circumstances, great cormorants sometimes raise 4 fledglings.

Care of young

Cormorant chicks may be fed less than half-an-hour after hatching, and by either parent although in some species the female delivers more of the very early feeds. The parent grasps the wobbling head of the tiny chick, an action which appears to elicit

more intensive begging or stimulates a recumbent chick. Many die in their first three days due to the difficulty of delivering food to one so small and uncoordinated; attempts to feed newly hatched chicks are often unsuccessful. Inexperienced adults lose more hatchlings presumably because less adept than experienced birds, though once chicks have grown, this discrepancy disappears. As in other pelecaniforms except tropicbirds, the chick inserts its bill into the mouth and throat of its parent (Figure 5.32). For the first few days the parent feeds them whilst brooding, raising a wing and turning its head under. Incidental stimuli, such as the arrival of a parent, or increased light, or cool air falling on the chick, may elicit begging. Adults seem able to retard or even arrest digestion when there are young to feed. Snow saw European shags regurgitate fish in an unaltered state one-and-a-half hours after their return. The flightless cormorant usually delays feeding the chicks for an hour or two after its return, possibly as anti-frigatebird behaviour. When chicks are large, the adult may arrive, deliver its food, and depart in less than half a minute. Feeding bouts usually last a few minutes during which the chick repeatedly inserts its bill. Younger chicks require more insertions per bout than older ones. As chicks



5.31 Comparative growth rates of cormorants/shags (brood size ignored).



5.32 Feeding technique, European shag.

grow, the average number of feeding bouts per hour drops. Significantly, single chicks of the double-crested cormorant were fed only slightly more often than each chick of a brood of three, indicating that the number of feeds per chick is not entirely dependent on brood-size (Dunn 1975). The sexes mostly take equal shares in feeding young but the female flightless cormorant may begin another cycle with a new male whilst her erstwhile mate continues to feed the fledged young.

Several cormorant species bring water to their young, as do pelicans but not other pelecaniforms.

Small nestlings are positioned on top of the webs by the adult using its bill and shuffling its webs. In panic departures chicks may be kicked out of the nest. For about their first fortnight, young cormorants are brooded more or less continuously, and then covered at night. Later, attendance is intermittent (flightless cormorants are exceptional in attending almost constantly for up to 40 days, but they

rarely forage more than 200 m from the nest). After about 14 days, the chick's thick black down enables it to keep warm. For the first three weeks or more the parent often shades the chicks with its wings. It preens them from soon after hatching until they are almost fully grown. From around six weeks most cormorant chicks are largely unattended and some ground-nesting species wander and form crèches.

In some species adults discriminate between their own and other young; in the European shag when chicks are four–five weeks old and capable of intruding.

Although they mainly defaecate clear of the nest, it soon becomes fouled. Food spilt during feeding may be re-swallowed by the adult but is sometimes placed outside the nest rim. Small pieces, together with soiled nest material are flung away using a sideways headshake. Some cormorants probe into the bottom of the nest, simultaneously quivering or shaking the head. This behaviour starts before eggs are

laid and continues throughout the nesting period; its function is unclear. It is not closely associated with the removal of soiled material, and is not followed by the sideways headshake used to fling away removed objects.

Behaviour of young

General

At first, young cormorants stand on their tarsi only when begging or threatening but at about three weeks they stand much of the time and by four move around if the site permits. From about two weeks, displaced chicks will climb back into the nest. They begin to exercise their wings, at first from a prone position, around week 3. At a month, European shags perform bouts of wing-flapping almost hourly, usually after preening. Snow noted that when they fed large young out of the nest, the adult first offered the back of its head, apparently as appeasement, although it attacked intruding young. As in other pelecyaniforms, adult behaviour patterns arise in the chick long before they will be used in their adult context. At two weeks the European shag worries nest material and at three, handles and builds with it. At the same time, upward gaping ('recognition') may be directed towards the incoming parent. Landing gape and sitting-gape plus bow occur later.

Sibling European shags of opposite sexes form attachments whilst in the nest, which on anecdotal evidence may persist through winter or beyond.

Play and 'curiosity' behaviour begin in the nest. Unusual objects may be mandibulated and passed from chick to chick. Moving objects such as insects elicit close attention and head-tracking, probably a stage in the development of hunting.

High-pitched begging and a squeaky 'complaint' call, uttered with closed bill by very young chicks, are their only vocalizations until threat calls develop. Males retain their calls throughout development whereas females, at least in some species, begin to lose their voice at 5–6 weeks.

Begging

The precise relationship between the chick's soliciting behaviour and the amount and frequency of

food delivered is not fully understood. This bears on the important issue of the extent to which adults control their reproductive effort. Very young cormorants are too uncoordinated to beg in a stereotyped way and the adults stimulate them to feed. Later, chicks perform rapid nodding movements which tickle the adults' inter-ramal skin, followed by touching and tracking the adult's bill-tip, accompanied by rapid, repetitive, and high-pitched calling which, with age, gradually drops in pitch.

Resting, sleeping, and thermoregulation

Downy young generally sit but may lie with head on nest. Feathered young sit or, increasingly, stand. They begin to adopt the sleeping position with bill in scapulars as their feathers develop. Temperature is regulated by gular fluttering, panting, and exposing the webs. The gular skin may be inclined upwards and eyelids closed to radiate heat.

Sibling rivalry

Cormorants rear broods of two, three or more. There are no known cases of obligative siblicide, though there is competition between siblings. It seems that the lower success of third chicks in broods of three, in the South Georgian shag (Shaw 1985), is due to parental withholding of food in the very early stages *before* food is limiting. If they survive this period, third chicks become adequate competitors for parental feeds.

Reactions to neighbours

Little information. In the great cormorant, large, feathered young may threaten neighbouring chicks when in close contact, such as playing with a piece of nest material. After leaving the nest they stand around waiting for the parents' return and chicks which attempt to gain a feed from a non-parent are pecked away. Well-grown young become aggressive towards intruding adults, sometimes mixing threat with begging; they lunge with open bill and head-sway (retracted) with occasional darting.

Crèching

Many species leave the nest before they can fly, either to wander and return or to gather in loose

groups. Crèches are less well developed than in pelicans. They have been recorded in, for example, European shag, crowned cormorant, double-crested, Brandt's, and even the arboreal pied cormorant, whose large young may gather on the ground, though this is probably before they can fly properly. Carter and Hobson (1988), observing Brandt's cormorants nesting on flat ground on SE Farallon, found that even small, relatively immobile young aged 10–25 days, from adjacent nests, huddled together in groups of 2–14, near to a nest-bowl. These 'nest-site crèches' occurred around the time that parents terminated continuous brooding. Parents present when neighbouring chicks attempted to join a crèche rarely interfered. Chicks moved from place to place and probably came together mainly at night, for warmth, since crèches contained most chicks at dawn and dusk. Chicks more than 20 days old formed crèches in their respective parts of the colony, between nest-sites or on the edge. They preened, slept, wandered around picking up pebbles etc. but rarely huddled. Crèches containing very large young, some able to fly, gathered nearer to the sea. These youngsters swam, dived and bathed, often then assuming the spread-winged posture. They were fed in the crèche, by their own parents, after they could fly.

Fledging

Even within a species the fledging procedure differs according to the type of nest-site (cliff-ledge or tree versus ground). European shags for which the sea was accessible on foot fledged at 55–8 days whereas those compelled to fly down remained in the nest several days longer (Snow 1963). In many cases, once down, they did not attempt to fly again for 10 days or more and most acquired flight when 60–70 days old. Similar behaviour is typical of cormorants. After entering the sea for the first time, young cormorants, like young gannets, bathe. In its first attempt to dive, the juvenile European shag puts its head beneath the surface and paddles vigorously, sometimes succeeding in getting just under, or even diving a foot or two, but it is another month or more before it dives with the upward

and forward leap of the adult. By the time it has been fledged for a few days it dives repeatedly but presumably without securing prey. Initially, dives are much shorter than the adults'.

A typical fledging period is 6–7 weeks but because it depends on habitat it varies between species. Most figures are highly approximate and not fully comparable. Some ground-nesting species leave the nest long before they can fly, and like pelicans may even take to the water though unable to fish for themselves ('Crèching' and Sp Acc). Others remain in the nest until they can fly adequately. The shortest period before free flight is *c.* 5 weeks (crowned cormorant); the longest *c.* 9 weeks (spotted shag). The range within the family is thus much less than in boobies and the length of the longest a mere fraction of the longest booby or frigatebird.

Post-fledging

All cormorants feed their free-flying young, but the duration varies considerably. Typically, it lasts 2–4 weeks, but a few species have been recorded feeding much older young. The newly fledged young of many species return to the vicinity of the nest to be fed, but later gather, often in numbers, on the sea-rocks or beyond the breeding colony proper. Only in the flightless cormorant is there known to be a clear division of labour between parents; the male feeds the fledged young whilst the female begins a new cycle with another partner. This is the reverse of the case in the magnificent frigatebird, the only other pelecaniform known to show desertion of the part-grown chick by one parent. There is no detailed account of the ontogeny of adult behaviour patterns.

Breeding success

Reasonably detailed figures are available for about 12 of the 39 species and even these are subject to the unquantifiable effect of human disturbance. Hatching success varies from *c.* 25–80%. Chicks fledged from hatched is similarly variable from *c.* 22–95%. Fledged from eggs laid varies from *c.* 20–60%, occasionally more. Cormorants rear from 0.3–2.5 young (average) per successful

breeding attempt, though some pairs may do considerably better. Breeding failure results from abandonment of breeding, starvation of young due to food failure, loss of eggs due to wash-out, infertility, conspecific interference, predation following human disturbance (a major cause in many), displacement of eggs, and loss of eggs or hatchlings due to parental inexperience. In Brandt's cormorant, Boekelheide and Ainley's (1989) unique figures showed that females aged 2–3 hatched 41% of eggs, whilst the figures for older females were: 4–5 years, 52%; 6–7, 62%; and 8–10, 65%. The corresponding figures for young fledged (from chicks hatched) were: 2–3, 31%; 4–5, 69%; 6–7, 79%; and 8–10, 81%. A comparable age-effect, though known in less detail, applies to several, perhaps most, cormorants. Predation is rarely a major problem. For example, South Georgian shag egg losses due to predation and accident together amounted to only 8%.

Figures for any species differ significantly between years and localities. In addition, productivity differs with clutch and brood-size which in turn correlates with age of female. Nevertheless, as a family, cormorants are more productive than tropical pelagic pelecaniforms or even pelicans. Within the pelicaniforms only anhingids and Peruvian boobies equal them.

Fidelity to colony, site, and mate

The fidelity of cormorants (a) to their natal colony, (b) to the colony in which they first bred, and (c) to their previous site and mate is intriguingly variable. Disregarding endemics, there are instances of notable natal philopatry among cormorants, as for example in the European shag, where on the Farne Islands (England) 78% of young returned precisely to the island of birth even though this was only 100 m from an alternative breeding area (Potts 1969). Yet there can be considerable immigration, leading to the rapid growth of a colony of this same species, as on the Isle of May (Scotland) (Aebischer 1995). Great cormorants in some localities tend to change the site of the breeding group from year to year, sometimes it seems independently of any obvious extrinsic factor such as disturbance. This trait is clearly incompatible with marked natal

philopatry. Yet some great cormorant colonies persist in precisely the same locality for many years.

The tendency to return to the same colony, once having bred there, is also variable; for example, in some European shags it is virtually absolute whilst in some great cormorants it is not. Fidelity to an exact site is unusual among cormorants even though there are instances, involving several species, where a site has been used twice or more. Similarly, long-term fidelity to mate is very weak.

Age at first breeding

Cormorants first breed when between two and five years old, usually two or three. Breeding during the second year (still only one year-old) happens occasionally in some species, for instance the pelagic cormorant. This short period of deferred breeding (a maximum of four years compared with 10 in the frigatebirds) reflects the family's less highly specialized feeding method, wide spectrum of prey, and inshore or inland food-rich habitat.

Non-breeding years

Like other seabirds, cormorants affected by major climatic perturbations such as ENSO do not attempt to breed and may even be unable to feed themselves. However, even in more stable areas, breeding effort can vary with year. For example, in some years, from 10–60% of European shags may fail to lay despite having bred in previous years (Aebischer and Wanless 1992). Up to 25% of experienced breeders may refrain at least once in their lifetime. This phenomenon, which occurs in most phalacrocoracids, possibly relates to feeding conditions, perhaps combined with social factors such as colony size, and with the condition of the birds by the time the breeding season begins.

Longevity and mortality

Few cormorants live more than 10–15 years, but potential lifespan is at least 20–30 in large species, such as the great cormorant. Mortality figures are often vitiated by human persecution and loss of rings (Wernham and Peach 1999 analyse the use of ring-recoveries in monitoring death rates and population changes); a mean of 10–15% per annum is

perhaps representative. In all species there may be considerable variation between years and/or localities. Adult annual mortality in the European shag may be as low as 7% (Sp Acc) but in unfavourable years a high proportion may die.

Mortality of cormorants in their first year and then before breeding is typically high. The few reliable figures suggest a pre-breeding mortality rate of 60–80%, most in the first year when they are particularly prone to starve or be shot or caught in nets etc.

Causes of death

A major cause is starvation-related illness through prolonged stormy weather or oceanographic phenomena such as ENSO. Although weather affects immature birds disproportionately, adults may die *en masse*. In April 1998, 19 of 20 bad-weather casualties in the Moray Firth were adults. Perhaps 5,000–10,000 starved on the Scottish E coast in Feb–March 1994 (Harris and Wanless 1996) leading to a 45% reduction in the breeding population of SE Scotland.

Exceptional circumstances such as toxins produced by ‘blooms’ of dinoflagellates (red-tides) can cause rapid and massive mortality. In 1968 and 1975, 82% and 62% of all shags breeding on the Farnes died within a few days. Populations would normally recover quickly but for overfishing and pollution.

Mortality due to starvation and stress is often compounded by sub-lethal infestation with parasites (see Hobson 1997, pelagic cormorant). Cormorants harbour many internal parasites and new species are regularly described. Heavy infestations of helminths—‘worms’, including nematodes (round worms), acanthocephalans (thorny-headed worms), cestodes (tapeworms) and trematodes (flukes)—have been found in double-crested cormorants (17 parasite species, Fedynich *et al.* 1997) and in great cormorants (11 species, Nasincova *et al.* 1993). Of European shags oiled after a tanker wreck (Shetland), 69% harboured sexually mature acanthocephalans (Munro *et al.* 1995). Subcutaneous tissues may be invaded by *Acari* (mites). Telfair and Morrison (1995) provide

details of parasites of the neotropic cormorant, including fleas and lice.

Newcastle disease, a serious threat to some cormorants, has been recorded in juvenile double-crested simultaneously in colonies in Canada (1990); in Canada and USA (1992) and (an epidemic) Saskatchewan (1995) (Kuiken *et al.* 1998; Kuiken 1999). In various parts of North America in 1992 it caused up to 80–90% mortality (Meteyer *et al.* 1997). It seems that different outbreaks are caused by the same epizootic virus. Avian cholera killed more than 14,500 adult-plumaged Cape cormorants in two months on islands off W South Africa. At Dassen Island, (greatest mortality) it killed 16% of the breeding population (Crawford *et al.* 1992).

Predation whilst foraging and at the colony, though varied, is probably insignificant at the population level. At sea, sharks kill some (e.g. flightless cormorant), alligators take neotropic cormorants, sea-eagles take European shags in Norway (62 of 1,044 prey-items were adult shags). At the colony, some are killed by mammalian predators such as mink and fox.

Man-induced mortality can be massive and affects many species (Chapter 4).

Anhinga/darter

Introduction

These large, attenuated, cormorant-like birds inhabit calm, vegetated, inland waters of the tropics and sub-tropics. They feed quite differently from cormorants. They are far less active in pursuit of prey, preferring stealth and a sudden, heron-like stabbing or grasping movement; an approach aided by their lack of buoyancy, and ability to remain mainly or totally submerged for relatively long periods. Although their display and general breeding biology strongly resembles that of cormorants they have been separated long enough to have evolved substantial differences in structure and morphology, though perhaps less so in ritualized displays. Their heads are small and necks and bills long and thin, giving them a snake-like appearance which is enhanced when they swim with body totally submerged. They like warmth and are birds of sunlit swamp, waterlogged riverine forest and

shallow lakes with clear water in which to feed among vegetation—as far removed from the haunts of some of their close relatives, the oceanic shags, as can be imagined.

Classification

There are good reasons why the darter and anhinga should be given family status, Anhingidae (Owre 1967), rather than placed within the cormorants as the sub-family Anhinginae. They are morphologically, behaviourally, and ecologically distinct and DNA–DNA hybridization suggests that they are as closely related to sulids as to cormorants, even though they look so much more like cormorants than boobies. Del Hoyo *et al.* (1992) provides a succinct introduction to the family and Johnsgard (1993) cites the main references on classification (Mayr and Amadon 1951; Vaurie 1965; Owre 1967; Olson 1985a; Becker 1986; Sibley *et al.* 1988; Sibley and Ahlquist 1990).

Like the other pelecaniform families anhingids diverged from common stock at least 30 MYA. Fossil darters of several species date back at least to the Miocene. Extant forms, however, are mostly regarded as belonging to two species, the anhinga *Anhinga anhinga* of the Americas and the darter *A. melanogaster* of Africa, the Middle and Far East, and Australia. The latter, largely on plumage, is often split into three species: African *A. rufa*, Oriental *A. melanogaster* and Australian *A. novaehollandiae*. Of these, *rufa* and *melanogaster* are most closely related.

The bird

Voice

Anhingids are generally quiet away from the nest. Adults of both sexes are able to rattle, hiss, click, grunt, and make loud or soft caws. The clicks of darters are ratchet-like, lasting up to four seconds and often given as the bird hops closer to its nest and prolonged and intense during disputes at a perching site. A rapidly repeated, rattling 'krr-r'r' ending with 'kururah' is given by both sexes when flying in to the nest and after landing. Comparable inflying vocalizations are common to all pelecaniform families except

tropicbirds. The hiss is associated with threat. Male darters utter an explosive 'khaah' (the anhinga's equivalent is guttural) during courtship including pre-mating; the female's version is said to be less harsh. Chicks squeak and click.

External features and anatomy

The silhouette is much like a large cormorant but with a distinctively elongated, snake-like neck terminating in a small, flattened head and long, thin, straight and sharply pointed bill quite unlike that of a cormorant. Anhingids often spear their prey whereas cormorants have a recurved tip for grasping. The cutting edges are finely serrated and the nostrils only partly occluded. The naso-frontal hinge allows upward movement of the upper mandible, thus increasing the gape. Presumably in relation to their spearing method of fishing, which does not call for a powerful grasp, the occipital condyle (to which is attached the muscle which pulls the mandibles together) is reduced in size and is cartilage rather than bone.

The unique feature of the anhingids is the special adaptation of neck bones 7–9, which allows the snap-like forward-darting of the head (Owre 1967). The eighth vertebra has its lower articulating surface facing backwards whereas its upper ones face forwards. This produces a Z-shaped kink in the neck similar to that found in herons, though in these birds the adaptation centres on the sixth cervical vertebra. The anhingids' thrusting to pierce prey is assisted by long tendons which run from muscles associated with the lower neck vertebrae and attach to the long, central spines of vertebrae 8–11.

The air sacs of anhingids hold less air than those of cormorants and they do not extend into the bones, which are particularly solid. Thus anhingids are even less buoyant than cormorants, which helps them in their stealthy progress through the water. The furcula (wish-bone) is not fused to the breast bone, a feature which presumably enhances flexibility. Despite this, and although the breast muscles are comparatively small at about 14% of total body weight (compared with almost twice that in frigates) anhingids are good fliers. Although the wings are

long and broad (anhingids soar well) their flight is dexterous, perhaps aided by the particularly long alulae and long, stiff tail, often widely fanned in flight. They are exceptionally good at climbing out of water onto branches, a very useful ability perhaps especially for chicks and pre-flying young. Some of their skeletal features appear to aid this. They have well developed knee-caps, a proportionately long femur which is straighter than in cormorants and presumably provides leverage, and a complete fibula, which may strengthen the lower leg.

The plumage is predominantly dark and the ventral feathers appear to be highly dissected, at times almost fur-like.

Locomotion

Although their short legs are set well back and they rarely walk they are nevertheless agile among branches and other vegetation, grasping with their prehensile feet and climbing adroitly. They are good at levering themselves upwards, hooking their neck over branches. Or they can flap-fly upwards. Apparently they do not usually choose to perch high in trees, preferring to be able, if alarmed, to slip quietly into the water, either diving in, dropping inertly or climbing down and belly-flopping. When alert they swim with body totally submerged and head and neck sticking out like a periscope.

They fly rapidly, tail fanned and alternating powerful wing strokes (about 4 beats per sec) with glides, often low over the water. They often soar to great height in thermals in company with storks, herons and ibises. They rarely (and then with difficulty) take flight directly from water. The long, broad tail and large wing area give them manoeuvrability necessary in swampy forest.

Body maintenance

Presumably similar to cormorants But Mahoney (1979) compared the anhinga and the double-crested cormorant with respect to their maintenance of body temperature and noted that cormorants maintain a significantly higher temperature than anhingas, that cormorants (wet or dry) have the same thermal conductance as dry anhingas, that anhingas retain much more water than cormorants when wetted and that at air temperatures

below their lower critical temperature anhingas lose more body heat when they are wet than do cormorants. This relatively lower efficiency may, she suggests, help to account for the more restricted distribution of anhingids.

Like cormorants they hang their wings out to dry which may serve, also, to raise body temperature after their plumage has become waterlogged. There is no information which would distinguish between sunning and wing-drying. Although Hennemann (1988) noted that anhingas spread wings in intense sun, this was after feeding. When loafing in sun they do not habitually use this special posture.

Moult

Unlike all other pelecaniforms, anhingids moult their flight feathers nearly simultaneously, rendering them flightless for a period. However, whilst the anhinga moults its tail about the same time as its wing feathers (Owre 1967) the darter apparently does so more gradually, starting with the central pair, followed by the two or three outermost pairs. Anhingas have a complete post-breeding moult and a partial pre-breeding one, in which the body-plumage is replaced (Palmer 1962).

Range and status

Both darter and anhinga are widely distributed (Figures 6.147, 6.148). The former is common or locally abundant in Africa, Asia, and Australia, and the anhinga, though considerably less numerous overall, is widely distributed in suitable habitat in South America and in North America mainly up to a line representing the 10°C isotherm, north of which it occurs in those few areas with a lot of December sunshine. Neither species is of conservation concern although drainage of habitat and local exploitation for food in parts of Asia have contributed to the decline or disappearance of the darter. Unlike some cormorants they do not habitually take fish of commercial value and hence are less persecuted by fishermen.

Movements

Anhingids disperse variable distances from their nesting areas. Anhingas nesting north of the 10°C

isotherm in a few favoured states migrate south during the colder months. Birds ringed in Mississippi have been recovered in Veracruz, Tabasco, and Campeche (Palmer 1962). The movements of darters are little known. In Australia both adults and juveniles disperse up to 2,000 km. During inland droughts they may erupt and move to coastal areas. In Africa, movements are reckoned to be merely local. In India birds are resident or they disperse locally if food becomes scarce.

Foraging and food

Anhingids are typically solitary feeders, although darters have been seen foraging in groups with individuals sometimes only a few metres apart. They submerge slowly with partly spread wings and extended tail, prior to stalking prey slowly, usually in mid-water and often among vegetation. Because of their solid bones and highly wettable body plumage, they swim very low in the water. They thrust with both feet when swimming underwater though alternately on the surface. The neck is held in a kink ready to dart the bill forward to spear prey (sometimes using only one mandible, sometimes both) which is brought to the surface, shaken free and swallowed head first. Fish often have two stab wounds on the ventral surface 5–25 mm apart. Their varied diet includes reptiles (snakes, turtles), amphibia, and invertebrates (Sp Acc), the latter often picked up from the surface. Owre (1967) found anhinga prey to be generally narrow-bodied, but Berkland (1978) did not find this in his study of darter prey.

In Assam, darters have been tamed and used to catch fish for man, just as cormorants are used in China and Japan.

Roosting, loafing and clubs

Although often solitary, anhingids are also sociable though without gathering in large numbers. They are more likely to loaf, sun, preen, and digest in the company of other waterbirds than solely with conspecifics. Breeders roost in the next tree, but otherwise darters roost solitarily or in groups, rarely as many as 100, in trees (often dead), bushes, and reeds, either at or away from foraging areas.

Habitat and breeding biology

Habitat

Anhingas prefer shallow freshwater, not too muddy and with emergent vegetation.

Darters similarly prefer interior wetlands, especially lakes and sluggish rivers but also estuaries and coastal waters with edge vegetation.

Colonies

Although they are gregarious, anhingids do not typically congregate in large colonies. These are often mixed (herons, egrets, ibises, spoonbills, etc.); in W Australia, pied and little black cormorants always nest near to *A. novaehollandiae* (Mees 1998). They also nest solitarily.

Frequency, timing and duration of breeding

Over their range as a whole, darters breed at any time of year though regions vary in the degree and timing of seasonal breeding (Sp Acc). The breeding cycles of anhingids are probably the shortest of any pelecaniform, requiring only about three months from beginning to end, which is less than a fifth as long as the longest pelecaniform cycle. The tendency for two widely separated peaks of laying in African darters has led to reports of breeding twice in a year, but this is not based on marked birds and needs confirmation, although of all pelecaniforms the anhingids would seem most suited to double brooding.

There are strong resemblances between cormorants and anhingids in the form of their ritualized displays (See Fig. at end of Ch. 5). Marchant and Higgins (1990) compare the darter's advertising display (wing-waving) with sky-pointing in boobies (though they erroneously include gannet sky-pointing which, in fact, is not an advertising display). They also equate the darter's recognition display 'snap-bowing' with 'crouch-bowing' in pelicans and 'head-jerking' in Abbott's booby. Such comparisons need detailed analysis but the general linking of these core pelecaniforms in behaviour is interesting. So far as is known the breeding behaviour of anhingas and

darters is essentially alike but there is no detailed comparative study (see Vestjens 1975 for the fullest account of social behaviour).

Territorial behaviour

The male selects the nest-site, defending a variably sized area (possibly the whole tree!) around it. Although overt fighting may occur, territories are maintained mainly by threat and display (Sp Acc). Accounts imply that the female, too, may defend the nest-site but whether solely against other females, and using the same behaviour as males, is not recorded. Apparently neither darters nor anhingas show appeasement behaviour.

Pair-formation

In its basic components the advertising display of the male anhingid, performed on or near the nest-site (which may already contain some nest material) strongly resembles that of cormorants, employing comparable wing-waving (= wing-flicking) movements and the equivalent of 'throwbacks' (Sp Acc). Prospecting female anhingas circuit the area and alight near to one or more displaying males who respond to her approach by displays which, again, are similar to the bill pointing and head waving of cormorants in the same context. The putative pair then display simultaneously.

Pair-bonding

As in some cormorants, sulids, and pelicans, the male anhinga may leave the site and circle the area in flight before returning and joining the female in 'recognition' or 'greeting' behaviour. Presumably darters behave similarly. There is nothing of substance to indicate that anhingids have diverged as far from the cormorants in behaviour as they have in morphology.

Copulation

The female crouches with lowered head and the male may seize her bill or place his head alongside; sometimes he grasps a twig. It lasts 4–9 seconds. The male anhinga may hold a twig and precede

mounting by wing-waving or bowing. He is said to grasp the female's bill and pull her head up whilst treading. Copulation continues for up to 8 days after pair-formation. In the darter it may continue into incubation (rare by 4th day after first mating) (Brown *et al.* 1982).

Nest

The male may begin building prior to pair-formation and material is collected from up to several hundred metres. Unlike many tree-nesting peleciforms, the female may break off nearby twigs or bring material and build, using sideways bill quivering. The male may participate even when there are eggs and young.

Egg/clutch

Both the darter and anhinga lay larger mean clutches (about 4 eggs) than any other peleciform. The brood grows more rapidly even than cormorants and pelicans and fledges at an unusually young age. This raft of characteristics is associated with their habitat and feeding habits (q.v.).

Replacement laying

Not recorded but likely to occur.

Incubation

Starts with the first egg and shared, possibly with slight male preponderance. Nest relief is most frequent early morning and late afternoon. The incomer vocalizes and the pair may display. The male usually brings nest material, the female more rarely. Like that of cormorants and pelicans, the incubation period is shorter than in the other peleciforms.

Chick, brood and brood reduction

There are differences between anhingas and darters in the colour of skin and down, but development is similar. In both species the average brood-size of chicks of various ages was about 3.0, the last-hatched

dying in some cases. Apart from the usual competition for food, which disadvantages the last-hatched, there is no mechanism for reducing the size of the brood (cf. boobies and pelicans). Growth is extremely rapid.

Care of young

Shared. See Sp Acc for details. Adults bring water and pour it into the chick's gape.

Behaviour of young

(See Anhinga Sp. Acc for details.)

Begging

The chick stretches with closed bill up towards the parent's head, whilst depressing and releasing the hyoid to produce squeaks and clicks. It will pick up food dropped into the nest as well as taking it directly from the parent's throat. It begs for water by holding the bill wide open. Chicks may beg to each other and even insert their bill.

Resting, sleeping, and thermoregulation

No specific details.

Sibling rivalry

Chicks compete aggressively for food and the larger young are favoured by the parents. There is no detailed information about the nature and frequency of brood reduction, but see below.

Crèching

There is no formal crèching unless the occupancy of the same branch by neighbouring chicks be so considered.

Fledging

At around 56–60 days the fledging periods are as short as any in the Order, though the precise age at which anhingids may be said to have fledged is difficult to determine. Chicks leave the nest and swim and dive when younger than any other pelecaniform, whether in response to disturbance or otherwise, and the likelihood of return probably varies

with age and other factors such as the difficulty of regaining the nest.

Post-fledging feeding

As fledging (difficult to define) occurs at a highly variable age, post-fledging feeding may also be difficult to define. Darters are not known to be fed by their parents after about 60 days, whilst anhingas are said to be independent by this age. If so, the total dependency period is shorter than in any other pelecaniform.

Breeding success

(See Sp Acc.)

Fidelity to colony, site, and mate

There is no precise information but the erratic breeding regime and the implications of comparative information from most cormorants indicate that anhingids are unlikely to remain faithful to site or mate for more than two successful seasons. However, del Hoyo *et al.* (1993) suggest that the pair-bond may last for 'years' and that birds can reuse the same nest each season. In some areas it is quite likely that a proportion of breeders will return to the same general area in successive years.

Age at first breeding

Not certainly known but very likely to breed at two years old and possibly in their second year.

Non-breeding years

No information but it is unlikely, given their particular breeding characteristics, that having once bred either anhingas or darters thereafter take years in which they do not attempt to breed.

Longevity and mortality

No information.

Causes of death

(See Chapter 4.) Predators include crocodiles (Africa) and large birds of prey (apparently Pallas'

eagle takes nestlings in India). Eggs and small young may fall to crows and other egg predators, but no information on scale of losses.

Frigatebirds

Introduction

Flight and feeding methods dominate frigatebird lives. Flight at sea, where they rarely alight; acrobatic flight in pursuit of other seabirds to make them disgorge; apparently idle flight, soaring high above the colony on angled wings, with delicate adjustments of the forked tail. No other seabird of comparable size is anywhere near as light. Frigatebirds feed entirely on the wing, and in the impoverished blue waters which many frequent this shapes much of their breeding biology, imposing a single-chick brood, protracted dependency, and low productivity. Successful breeding is accomplished, on average, only once in several years. This productivity, perhaps as low as in any bird, implies a long life if populations are to remain stable. It means that loss of breeding adults, for example through human persecution, could lead to irreversible decline before this became apparent. Considerable reduction in most or all species occurred in the 20th century (Chapter 4).

The breeding biology of frigatebirds is unusual in other respects, amongst which are specialized methods of pair-formation and a puzzlingly high incidence of conspecific interference at breeding colonies, which contributes notably to low breeding success.

Classification

Frigatebirds date back at least to the early Eocene (53–48 MYA, Chapter 1). Extant forms comprise the single genus *Fregata*, containing five very similar species. Formerly, only two were recognized. Of these five, though not without dissent, the great frigatebird has been split into five sub-species and the lesser and magnificent frigatebirds each into three sub-species. Relationships within the family, and more widely within the *Pelecaniformes*, of which (with the tropicbirds) it is an aberrant member, are discussed in Chapter 1.

The bird

Voice

Frigatebird noises are a confusing mixture of vocal and apparently mechanical sounds and it seems helpful to compare species here. They squeal, grate, gakker, warble, chuckle, reel, twang, drum, quaver, and rattle, clap, or clack their bills. Many of these noises are separable by context or according to their vocal or mechanical nature. Away from the breeding colony they are mainly silent, although when chasing they may utter grating calls. The male's sexual advertising display is similar in all five species but the accompanying vocalizations differ. The great frigatebird utters a high-pitched warble (yodel or whinny)–'hoo-hoo-hoo'. It lasts about three secs per warble and several may follow in quick succession. In the larger Christmas frigatebird it emerges as a slower and deeper 'ee-ow, ee-ow, ee-ow' which, when played faster on a tape recorder is higher pitched and sounds just like the great frigatebird's version. The other three species reputedly lack this vocalization. According to Reville (1980) the lesser frigatebird does not vocalize when advertising, whilst Diamond (1975a) says it produces only mechanical sounds (though elsewhere in the same account he says it utters a rapid



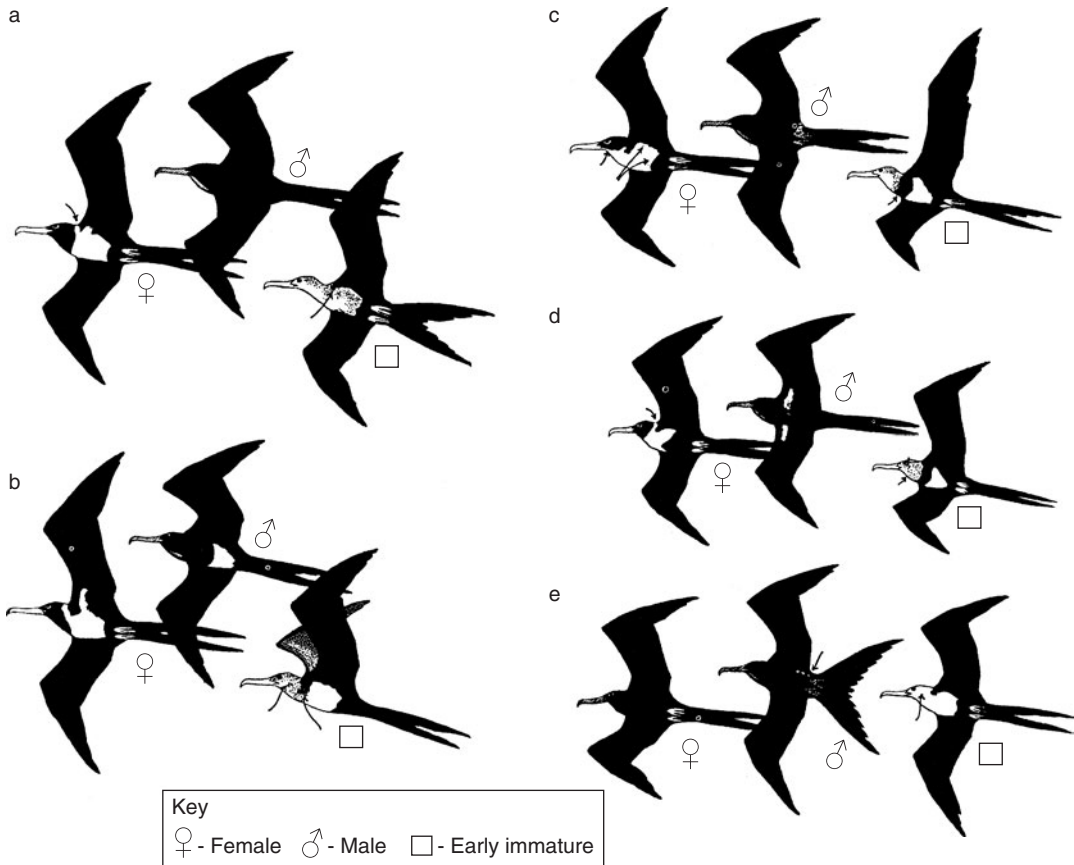
5.33 Shape and flight. Juvenile great frigatebird chasing adult male with nest material.

whistle). The Ascension frigatebird (Stonehouse and Stonehouse 1963) bill-clatters but vocalizations are not described. The magnificent frigatebird produces a resonant drumming when its pouch is inflated. It seems unlikely that in such a closely related group there will be a fundamental difference (vocal versus mechanical) in the sounds accompanying a clearly homologous display, and an adequate comparison is overdue.

The great frigatebird intersperses its warble with a fine-drawn 'fisherman's reel' sound, with parted mandibles. This is probably mechanical. In full display the magnificent frigatebird alternates reeling with drumming but can reel even with deflated pouch. Lessers also reel (Diamond) though not

according to Reville. Mandible clacking or clattering is common to all displaying male frigates. Females are much less vocal in the context of display.

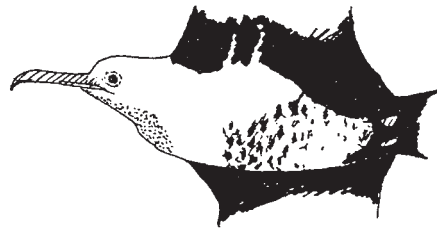
The other main context for frigatebird vocalizations is post-landing. The male great calls 'clew-clew' or 'teeu-teeu' with a twanging quality, whilst the female has a more guttural 'wiick-wiick-wiick'. Males use a similar 'wick' call, sometimes mixed with warbling, in aggressive situations. The lesser's equivalent is a series of short whistles in the male and a hoarse 'chuck-chuck' in the female. In the magnificent (both sexes) it is a rapid rattle decreasing in pitch and increasing in speed. Incoming Christmas frigatebirds utter a deep, hoarse disyllabic call.



5.34 The external features of frigatebirds. a. Magnificent frigate, b. Christmas frigate, c. Great frigate, d. Lesser frigate, e. Ascension frigate (From Nelson 1976, drawings: J.P. Busby.)



Great



Magnificent



Magnificent



Great

5.35 Stages of immature plumage in magnificent and great frigatebirds. Cinammon colouration is diagnostic of the great frigatebird. The abdomen mostly fills with black before black appears on the head. A bird with black on the head at this stage is a magnificent (lower left). (From Howell 1994.)

External features and anatomy

The frigatebird silhouette is unmistakable (Figure 5.33). Characteristically, the narrow, pointed wings are held sharply angled above body level, giving an open W profile. This shape is less stable than a broad, flat, slightly upturned wing and facilitates the aerial acrobatics for which frigatebirds are renowned. Of the 11 primaries, the outermost is vestigial and primary 10 (second outermost) the longest. There are about 23 secondaries. The characteristic wing shape is due partly to the short humerus. The length of the wing derives mainly from the radius/ulna and the long primaries. Despite the wing's long, narrow and pointed shape (aspect-ratio 12.8), loading is extremely low because frigatebirds are so light. A span of up to 244 cm may support a weight of around 1.5 kg. The highly pneumatic bones of the skeleton may weigh only about 5% of the bird's total weight whereas feathers (mostly wing) comprise some 22%. The magnificent frigatebird has a buoyancy index, relating weight to wing measurement, of

5.28, which is nearly twice that of some cormorants. Pennycuik (1983b) gives a wing-loading for the magnificent frigate of 36.5, compared with 57.8 for the brown pelican. Thus soaring flight is virtually effortless and can be maintained for long periods at little cost, enabling them to watch for prey, including victims for piracy. When foraging at sea, such low-cost flight facilitates search for appropriate sea-surface indicators of prey. As a further adaptation for soaring, the pectoral girdle gains rigidity by having the furcula fused to the sternum. The latter is deep-keeled for the attachment of the powerful pectoral muscles which weigh 15–20% of total weight. These power the deep, muscular strokes which produce startling acceleration and excellent hovering ability. In normal flight in calm air, magnificent frigatebirds beat their wings at about 2.8 per sec, giving a speed of 9.3 m/sec (33.5 km/hour) (Pennycuik 1983a, 1983b) in straight flight. This compares with 8.67 m/sec when gliding and 6.22 m/sec when slope soaring. Although Pennycuik says that 'take-off' appears to be possible only by dropping from an elevated

perch, not from the ground or water-surface' simple observation (like the bumble-bee's flight) defeats theory, since great frigates, at least, are perfectly capable of the latter, even in calm conditions (personal observation).

The tail, 12 tail feathers with the fork produced by elongation of the outermost, constantly changes shape as the bird manoeuvres. According to Balmford *et al.* (1993) long, forked tails are 'aerodynamically optimal'. The rather small, rounded head is usually held well retracted and, in ordinary flight, never stretched forwards. The vestigial legs and feet are usually hidden in the abdominal feathers and do not disrupt the slender, streamlined shape. Females are considerably larger than males and there are variations in size even within a species and in the same ocean— for example great frigatebirds on Johnston Atoll (PO) were heavier and had proportionately shorter wings and tails than birds on Christmas Island (PO) (Schreiber and Schreiber 1988).

Although the magnificent and Christmas frigatebirds are nearly 40% bigger (overall length) than the lesser, which is the smallest species, all frigatebirds are large, mainly black birds with, in most cases, some white on the female's ventral surface, the pattern varying with species. Murphy wrote (1936) 'Man-o-war birds exhibit specific differences which should be the delight of a geneticist . . . every adult wears a plumage representative of a stage in the ontogeny of some other man-o-war. It seems probable that all the forms in the world are very closely related and have differentiated through genetic mutation which has affected the size, proportions and plumage-patterns of each'. All adult males have an iridescent green or blue gloss, especially on scapulars but also on head and back. Apart from some cormorants, no other pelecaniform has this.

Juvenile frigatebirds are pale beneath, with rufous on head and neck, a dark pectoral band, and a white abdomen. The alar bar, though variable in width and colour, is pale and conspicuous. The rufous colouration varies in pattern, amount, and intensity, and the black pectoral band fragments at varying rates, even in the same species, and may make identification next to impossible. Apparently, the alar bar is neither produced nor enhanced by

feather wear but, on the contrary, can be diminished by the attrition of the white edges to the feathers of the brown wing-coverts which form the bar.

Frigatebirds lack gaudy facial skin but that of the throat and between the rami of the lower mandible produces in all courting males an enormous scarlet balloon decorated at the edges with a few small feathers which, incidentally, can be mapped to allow individual identification. The gular sac is inflated by a pumping action which forces air from the trachea, through a small lumen. The sac of one individually marked frigatebird took 19 days to develop from shrunk orange to inflated scarlet, but once attained, a full sac can be deflated and re-inflated in an hour or two. The sac may be elongated-heart-shaped, fat-cylindrical or more spherical. Occasionally the male flies with the sac partly or even fully inflated, which renders the passing booby, however fish-laden, perfectly safe.

The orbital ring is bright red, blue or blackish. It varies, not only between species but, in great and lesser frigatebirds, between populations of the same species. Again, detailed categorization is lacking. Generally, the bill is grey-blue or blue-black but in the female Christmas frigatebird it is pink. Coincidentally, exactly the same sexual dimorphism in bill colour occurs in that other Christmas Island endemic pelecaniform, Abbott's booby. Frigatebird bills are long, thin, and sharply hooked with a noticeably wide and flattened saddle towards the base. This strengthens it against the fierce resistance which applies when, with downbent head and in full flight, the bird whips its bill through the water to snatch prey. At the same time the thinness of the distal portion confers minimum impedance. Presumably because it is the hooked tip which secures the prey, the cutting edges of the mandible are plain whereas in the plunge-diving sulids they are serrated. The external nostrils are thin slits. Bills are wielded with astonishing precision; in full flight, a frigatebird can clean up a thin smear of fish from rock or whip a morsel from sand without leaving a mark.

The pelvic girdle, required neither for swimming nor walking, is greatly reduced. The fibula is completely fused to the tibia. The short feathered tarsi are scarcely visible in perched birds and, with the vestigial feet, are useless for walking. The webs

are totipalmate but much reduced and thus less of a handicap in perching. Frigatebirds can swim though they rarely do. The flexible toes and sharp claws give an excellent grip on twigs. The flange of the middle-toe claw is serrated and used for scratching and raking. They do not possess a brood patch. The oil gland is feathered.

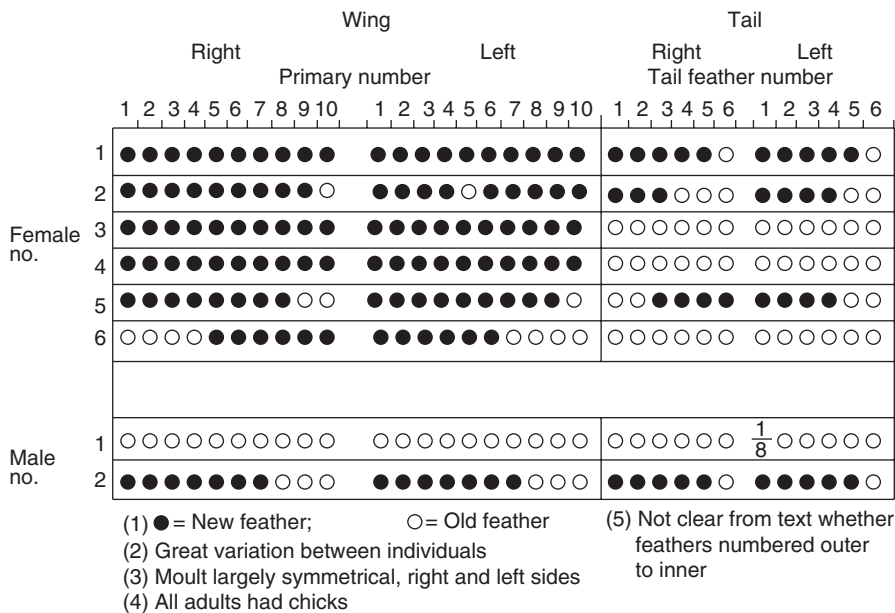
Locomotion

Frigatebirds comparatively rarely alight on water (their aerial feeding method makes it unnecessary) and never for long, but they can take off from it even in calm (personal observation). When not airborne they usually perch above ground level, but they do not move around, even in trees. They remain on top, or at the edges, of vegetation. Tree-nesters may require considerable airspace for free fall. Often they have to take off with the wind because they prefer to alight into it. Where wind direction is reasonably consistent during that part of the breeding cycle when there is most coming and going, they nest on the lee side of trees.

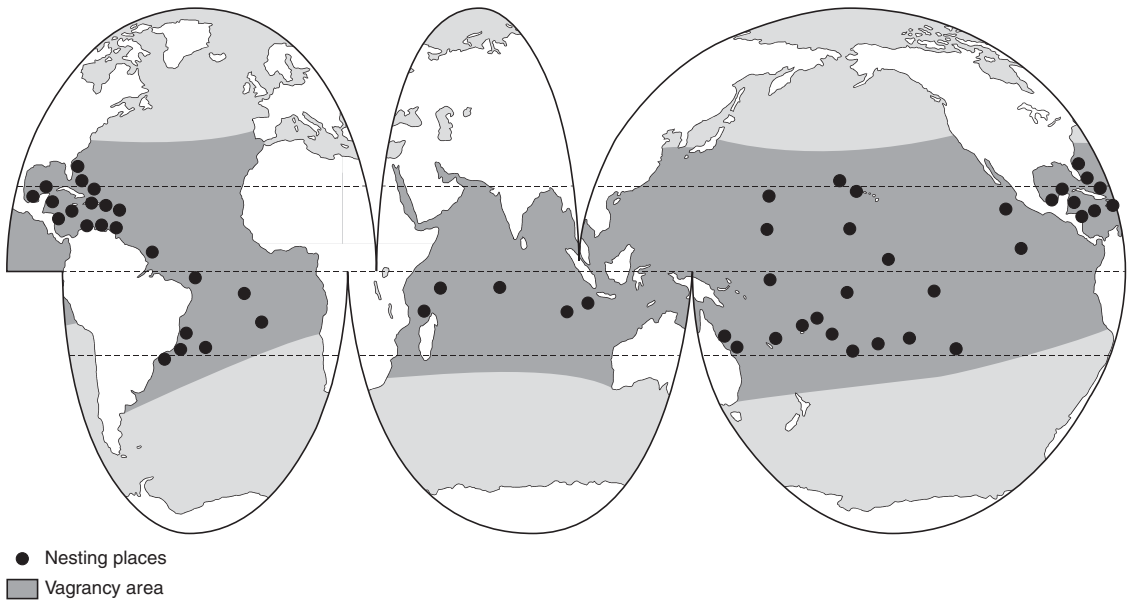
Body maintenance

Frigatebirds bathe in flight, splashing with their bodies without settling. Although they possess an oil-gland their plumage is wettable. Often, they preen on the wing. They scratch their heads directly (underwing) in flight but indirectly (overwing) when perched. Other pelecaniforms scratch only directly. They drink on the wing and like to sip fresh or brackish water, swooping low and delicately dipping their bills. Frigatebirds sleep with retracted neck, bill inclined forwards and downwards, or with head hanging, but less commonly in the usual pelecaniform position with bill buried among scapulars.

Incubating frigatebirds may face severe problems of heat control. Great frigatebirds on Midway absorbed >90% of solar radiation and yet remained on their nests, without water, for up to 16 days (Mahoney *et al.* 1985). Despite air temperatures as high as 33.3°C and an 'environmental temperature' (an index of heat load) up to 51.7°C, the birds maintained a body temperature of around 39.3°C. They reduced heat by gular fluttering and by erecting the



5.36 The moult pattern of the great frigatebird in the Galapagos. (After Coello *et al.* 1977.)



5.37 Distribution of the world's frigatebirds. A tropical family. The dissemination of frigates into the Atlantic may have taken place through the Panama Isthmus and around southern Africa. (From Nelson 1980, after Shuntov 1974.)

dorsal feathers, especially the scapulars, whilst drooping the head below the body until it was in the shade.

Sunning

Uniquely among pelecaniforms, frigatebirds upturn the undersurface of the outspread wings towards the sun, or drape themselves over rocks with their backs to it. They adopt these bizarre wing-spread postures, sitting back on their tails in blistering sun and (Galapagos) among hot black lava. At times they appear to be heat-stressed, gaping and panting. The head may be held normally or drooped low. They do not sun in this way on the nest although they may adopt an energy-saving posture (see above).

The probable function is not, as sometimes suggested, to lose body-heat. Why, in such a case, would they choose full tropical midday sun and the hottest substrate, when shade is available? Nor is it likely to kill ectoparasites. Most probably it is to restore deformed flight feathers to their optimal shape. Houston (1980) showed for vultures that the

pressure of air during prolonged soaring bends the primaries upwards. This curvature can be remedied by subjecting the keratin of the feathers to considerable heat, which restores its molecular configuration. It is possible, too, that under breezy and somewhat cooler conditions, armpit moisture could be lost via evaporative cooling. The two functions are not mutually exclusive, but in a bird as reliant on flight as the frigatebird, wing-feather shape is critically important.

Moult

This is typically pelecaniform, with two or three generations of flight feathers coexisting in the same wing, some abraded, others still perfect, and yet others new or erupting. Adult wing moult may be delayed until their offspring have fledged (though still dependent), then resumed nearer to the end of the breeding cycle. Coello *et al.* (1977) give details for six female and two male great frigatebirds, all with chicks, from Tower, Galapagos (Figure 5.36).

Range and status

The Christmas and Ascension frigates are island endemics. The great and lesser frigatebirds are pan-tropical, largely Indo-Pacific, nesting in the Atlantic only on Trinidad and Martin Vas. Commonly, they nest in the same archipelago but on different islands, but sometimes, as on Aldabra (Seychelles) and North Keeling of Cocos Keeling they nest on the same island, though never in homogeneously mixed colonies. Often two species nest on the same island, most commonly great and lesser. Extremely rarely three species may do so. Thus Christmas Island (IO) holds great and Christmas frigatebirds but only a very few lessers, which, if they occurred, had been overlooked until recently (Stokes personal communication).

The magnificent falls between the island endemics and the cosmopolitan great and lessers both in world numbers and its restricted distribution. It breeds in the tropical eastern Pacific from Ecuador and central Galapagos Islands to Baja California, and in the Atlantic from Brazil to the Cape Verdes and the Gulf of Mexico.

Movements

The global distribution of frigatebirds bears an (imprecise) relationship to trade winds, which blow consistently, unlike air-currents which depend on daily heating and cooling of land masses. Throughout their protracted non-breeding period, adult frigatebirds, as also immatures, are mainly dispersive, sometimes for several thousands of kilometres despite their (presumed) inability to rest on the sea. They may roost in hundreds or even thousands, on islands where they never breed. But adults may remain within their breeding range even if not near to their own colony. In the great frigatebird at least, many, or perhaps most individuals at some colonies are transitory rather than breeding. Of 703 birds of various categories ringed on Kure Atoll (PO), relatively few were recaptured there and many 'inter-islanders' were handled (Woodward 1972). Furthermore, the twice-monthly estimates of numbers on Kure, where there was a winter exodus, ranged from a mere 15 in December to 1,500

through May/June. A Lincoln-index calculation put the Kure population at 7,700 birds which, though probably too high, demonstrates that the breeding population of 10–400 pairs is a fraction of the total number using the island. Similarly, the Aldabra population of great frigatebirds drops significantly for part of the year (Diamond 1975a). But on Christmas Island (PO) the number of great frigatebirds did not vary significantly through the year (Schreiber and Ashmole 1970). Such differences may be associated with regional climate and oceanography but apart from obvious disadvantages such as low temperatures, wind, and rain, which coincide with the frigatebirds' disappearance from some areas, there are few records of their distribution at sea and little on which to base interpretation. Recoveries of marked birds demonstrate the scale, but not the frequency, of trans-oceanic movements. Thus a lesser frigatebird from Aldabra was recovered 4,400 km to the NE less than a year after independence (Diamond 1975a). Four adult female great frigatebirds, apparently breeding on Kure when marked, were recovered far to the west, three in the Philippines 6–7 months after handling and one in the Marshall Islands after 11 months. Other adults marked on Kure were recovered on central Pacific islands; birds marked as sub-adults were twice as likely as adults to be recovered on other islands (Woodward 1972). Sibley and Clapp (1967) record 79 recoveries from central Pacific islands. Most had fledged 3–10 months previously ('fledged' presumably meant 'had become independent'). Such newly independent great and lesser frigatebirds disappear from the immediate vicinity of the breeding colony, returning when about two years old but still in immature plumage. Magnificent frigatebirds disperse northwards from their Caribbean and Bahaman colonies and are regular along the Atlantic and Pacific coasts of America, far from any breeding haunts. Their movements correlate reasonably well with their breeding regimes in the above areas (Palmer 1962). Thus they regularly appear along the gulf coast in June, increase July–September and then tail off (the main laying period in the Caribbean and Bahamas is late October–February). However, it is impossible to determine the status of adults seen on passage. Some may

be failed breeders, of which there are many, others may be adults that have bred successfully, yet others may be adults taking 'rest' years.

There is too little information about Christmas and Ascension frigatebirds to categorize their movements, but the former range widely in the SE Indian Ocean and seas north of Australia.

Foraging and food

Although largely diurnal, frigatebirds are active on moonlit nights, including feeding their young. Typically they leave the colony or roost soon after dawn, trickling to sea rather than in the purposeful phalanxes of the red-footed boobies with which they habitually associate. At a large colony there may be hundreds of birds circling apparently aimlessly but often gaining height in thermals. Later in the day they may circle at medium height ready to intercept incoming boobies and other seabirds.

Although breeding birds often forage fewer than 100 km from the colony, frigatebirds (status unknown) may be encountered many hundreds of km from the nearest breeding locality. If they can remain aloft for days on end (conjecture) their foraging range would be enormous, but at present there is no radio-telemetric tracking data akin to that for the great albatrosses (e.g. Weimerskirch *et al.* 1993). Local availability of food must determine some frigatebird foraging but, at least during incubation, the off-duty great frigatebird (Galapagos) may be away from the nest for more than a fortnight. However, birds with chicks often return to the colony every two or three days or even more often. On Aldabra, the chicks of great and lesser frigatebirds were fed every day or day-and-a-half (Diamond 1975a, Reville 1980). In the Galapagos, magnificent frigatebirds fed chicks every day or two (Coello *et al.* 1977). Fully grown or free-flying but dependent young must often endure long periods without food and, at least on Tower in 1964, some of the latter died of starvation (Nelson 1968).

Foragers have to replenish their own reserves as well as collect food for their offspring. The longer the period of prior fasting, up to 17 days during incubation, the longer the restorative period. A feeding

absence of a fortnight need not mean that the bird has travelled far from the colony, and longer absences do not mean a *pro rata* increase in the amount delivered to the chick. This depends, among other things, on the food-carrying capacity of the adult and on the capacity of the chick to accommodate parental feeds. Near-simultaneous visits by both parents may overtax the chick's ingestive capacity and result in a missed feed.

Frigatebirds snatch prey from the surface layers and catch airborne flying fish. Often they beat back and forth, gliding down or plunging precipitately to the surface before checking abruptly. They rarely dip more than their heads; they are not splash-plungers. Often they sweep over the surface at speed, inclining their bills at right angles or more to the body axis. They may feed with boobies, terns and shearwaters, benefiting from prey driven to the surface layer by predatory fish such as tuna (Au and Pitman 1988). Flying fish figure prominently in the diet. Locally, several others such as *Brevoortia* sp may be important. Ommastrephid squid, plankton and jellyfish are taken too (Sp Acc).

Frigatebirds take eggs, and chicks of other seabirds, and newly hatched turtles. Predation on their own species, however, although frequently reported, is related to prior disturbance, usually by man. Such predation on eggs and small chicks should be distinguished from conspecific interference in which eggs are displaced and chicks killed but not eaten, and which occurs in undisturbed conditions.

Kleptoparasitism

All five frigatebirds pirate several other seabirds, most commonly boobies (all species) but also smaller victims such as terns, tropicbirds, and shearwaters, and even each other. They operate singly or in groups, often out at sea but mainly at the breeding colony, where a stream of homecomers provides a dependable source. Chasing appears to be triggered by various stimuli; great frigates will chase and kill young shearwaters even though they can neither swallow them nor settle on the water to tear at them. Frigatebirds hound their victim with speed and dexterity, upending it by wing-tip or tail until it regurgitates. Competing to snatch the food, they often chip and

scratch their victim's bill. They seem able to discriminate between full and empty incomers; possibly an initial approach elicits vocalizations which, because of food pressing on the syrinx, sound different in full birds. Gilardi (1994) did not see any of his marked breeding great frigates chase. As with the frigatebird's more usual feeding technique, kleptoparasitism may require a long time to perfect and immatures are less successful than adults (but see below). Even in imperfect form it may help a few immatures over a difficult period and a few successes could be critical to survival. However, frigate birds may coexist with but ignore large fish-eating birds. On Barbuda, magnificent frigates appeared not to chase brown pelicans (Diamond 1973).

Several observers have documented various parameters, including sex and age of the chaser; success (though this may be a somewhat imprecise statistic); single against group chases; effect of group-size of the victims and of height on approach to the colony.

Apparently females—which prefer boobies and tropicbirds whilst males (smaller) may prefer smaller victims—chase more than males. Of 2,048 chases, mainly of blue-footed boobies by magnificent frigatebirds on Isla Isabel (Mexico), 1,553 were by females, 162 by juveniles, and only 8 by males (Osorno *et al.* 1992). In the Caribbean, females chased more than males (Diamond 1978). The great frigatebird showed a similar sex-bias (i.e. females chasing more than



5.38 Breeding habitat (*Cryptocarpus* shrub) of the great frigatebird on Tower Island, Galapagos. Note the free-flying juveniles (white heads) from eggs laid the previous year.

males) in Hawaii (Cummins 1995), British Honduras, on red-footed boobies (Verner 1961) and on Christmas Island (PO) (Schreiber and Hensley 1976). On Europa (IO) females accounted for 82% of 517 chases (Le Corre and Jouventin 1997a). However, on Tower (Galapagos), males chased more (Nelson 1976). On Aldabra female lesser frigatebirds chased more than males (Diamond 1975a).

On Isabel, 91 female magnificent chases (of blue-footed boobies) produced a regurgitation but only 58 (3.7%) resulted in food for the pirate; Heerman's gull often snatched the reward. Surprisingly, juveniles were about as successful as females. On Aldabra, 18% of lesser frigatebird chases of red-footed boobies were successful whilst great frigatebirds succeeded on about 18% of occasions; on Midway adults were more successful than immatures (Gilardi 1994). Elsewhere, this frigatebird had 12% success (Galapagos) and a highly anomalous 63% on Christmas Island (PO). On Europa (IO), success of great frigatebirds again on red-footed boobies was 11% during the boobies' breeding period and 19% outwith it, producing a risk of only 0.4% and 1% respectively of an individual booby losing its food (Le Corre and Jouventin 1997a). A low impact on the host population seems typical of all such interactions and this may be necessary for a stable relationship. Group pursuits were three times as successful as individual chases on Isabel, as they were also in the great frigatebird on Midway (PO) (Gilardi 1994). Group-size of the masked boobies returning to Henderson Island had no significant effect on the likelihood of being chased, though big groups tended to return higher and this helped to save them (Vickery and Brooke 1994). The figures for success suggest that, except for a few specialists, kleptoparasitism is not very significant energetically; probably less than 5% of daily energy requirements are met by piracy though a few individuals may obtain substantially more (Vickery and Brooke 1994). Probably only a small proportion of the population practise it or individuals are kleptoparasitic for only a fraction of the time.

Roosting, loafing and clubs

Frigates prefer to roost or loaf in trees or bushes but will use rocks or beaches. Many breeding birds

roost within the breeding area but distant from their nests. Sometimes they loaf among immatures and non-breeders. But many of the frigatebirds loafing or roosting within a breeding colony are not breeding there. Diamond (1975a) estimated 14,000 such birds in the mixed colony of great and lesser frigatebirds on Aldabra. Although they are gregarious the gatherings are made up of small groups and lack social structure or behaviour. They do not contain free-flying but still-dependent juveniles, which at first roost near to their nest-site and if displaced by displaying males consistently roost nearby, where they are fed. Magnificent frigates roost and loaf sometimes in hundreds or even thousands often far from nearest colony, mostly in trees but also on man-made structures or even on beaches. Frigatebirds seem not to gather in clubs.

Habitat and breeding biology

Habitat

Frigatebirds are tropical marine, often pelagic seabirds. They often feed close to the nesting island and the magnificent, especially, feeds inshore. However, frigatebirds have been encountered hundreds of kilometers from land, although there is no proof that they were breeders. Presumably because of their feeding habitat they prefer to nest on oceanic islands. They utilize whatever trees or shrubs are available, from ground-hugging zerophytes to tall jungle trees. Even mainly dead trees are used by Christmas frigatebirds. Perhaps most often, they nest in mangroves. In the absence of cover they can nest on cliffs, rocky outcrops or even (Ascension frigatebirds) on bare ground, from which, given some wind, their lightness and enormous wing span enable them to rise.

Colonies

Like those of most pelagic seabirds, frigatebird colonies may be extremely large. As the pattern of settlement shows, they are made up of clusters of nests. To an overflying frigatebird each cluster tells a story. It has a size, a spacing in relation to other

clusters and, within it, a 'behavioural profile' imparted by the frequency and intensity of display. The whole forms a complex stimulus, different for each species, which directs the responses of the overflying individual. These features are detectable by the human observer only by minute attention to detail. Reville (1980, 1988, 1991) showed that the apparently minor behavioural differences between frigatebird species, in this instance great and lesser on Aldabra, are related to differences in their ecology, in that the dynamics of the cluster (its size and the way it forms) affect breeding success.

Frequency, timing, and duration of breeding

In general, and despite protracted laying periods in all species, egg laying is broadly seasonal. However, the extreme length of a successful breeding cycle, which may take considerably more than 15 months, means that some part of it has to be conducted in every month of the year, even if some months are climatically or otherwise unfavourable. Presumably, the most energetically demanding phases are conducted in the most propitious periods, though where these are imprecisely predictable, a broad spread of the demanding phases should be adaptive. Analysis of the relevant parameters would be difficult and has not been attempted. In general, frigatebirds can breed successfully only once in every two years, or even less often if they take 'rest' periods.

There is still no detailed ethological study of any frigatebird, although Reville's seminal account of spatial aspects of nests in great and lesser frigatebirds includes by far the most complete account of breeding behaviour. Reville's is the only study in which the behaviour used in site-establishment and spacing is described for individually recognizable birds.

Territorial behaviour

Frigatebird territoriality is highly unusual. In all other pelecyaniforms, with the partial exception of some pelicans, a territory is established and defended before pair-formation. But in frigatebirds, near to or even on nests which are *still* in use by adults and their free-flying but dependent offspring from the previous year, 'new', pre-breeding males come

together to display to overflying females. Until one realizes this, the situation appears totally confusing (see Nelson 1968, 1976).

Males advertise for females by presenting their inflated gular sacs in a highly ritualized display. However, they may move around, which means that (unlike most other pelecyaniforms) the site on which they display may not become the eventual nest-site. They do not first establish a breeding-site in the normal sense and remain there until successful in attracting a female. The nest is eventually built on the site at which the female definitively joins him, but before that he may have moved from one display cluster to another, or, within a cluster, from one display site to another. In the great frigatebird, success in attracting a female increased with cluster-size, implying that enhanced visual stimulus is important. Displaying males may cluster so densely that they touch each other. Clearly, it would be maladaptive to defend a display-site before a female had accepted him on it and it had thus become a nest-site. I claimed that they lack 'orthodox' territorial behaviour, that is, overt fighting and ritualized site-ownership display. The former is incorrect for the great frigatebird on Aldabra. There, where a male occupies a platform (usually one that he did not build) he may be challenged and overt fighting may ensue. Reville recorded frequent fracas involving 'tangled melees of up to seven males on a nest platform', especially late in the laying season. Males, of unknown status but including some with faded orange gular sacs, continued to grapple and supplant each other on vacant nests even when courtship and egg-laying in the colony had mostly ceased.

There was competition for position within clusters of displaying males; supplanting was frequent and involved threat and sometimes overt fighting. Males suffered scratched and bleeding gular sacs and one encounter caused serious eye injury. On two occasions a male fell into the water and was taken by sharks. Always, the competition was between males for a site within a display cluster, that is, for a socially adequate site rather than simply a physically adequate one. Thus competition occurred even when there were alternative sites available, many of which later received nests. That males did not simply settle at the edges of a cluster

may imply that a more central position is an advantage. But spacing within clusters tended to be regular and males attempting to get in were resisted. Nevertheless, in the great frigatebird, overt fighting is not the main arbiter of spacing; often, it merely leads to a free-for-all.

Lesser frigatebirds seem less aggressive. During 556 hours of hide observation Reville did not see a male with a sac threaten or attempt to displace another male on a display site, though he recorded more than 200 such instances in the great frigatebird. Indeed, on Aldabra, great frigatebirds often supplanted lessers on their nests and in two cases killed young aged 2–3 weeks. They then displayed on the nests and attracted females.

Magnificent frigatebirds defend display sites by bill-snapping and jabbing (Diamond 1973). Sometimes a male uses the sexual (advertising) display–gular presentation—in response to intrusion by another male. The great frigatebird also does so on occasion but apparently lessers do not.

No frigatebird has a special site-ownership display, regularly proclaiming that the site is occupied and will be defended. The territory is merely the nest and even the landing perch is neither exclusive nor defended. Nor is the site maintained in successive breeding attempts. Given the nature of pair-formation, site fidelity would be impracticable.

Pair-formation

Where two or more frigatebird species are sympatric, which can happen with all except the Ascension, the different patterns of black and white on the female's undersurface may guide males to display to the correct overflying female. Only in the Ascension frigatebird does the female lack distinguishing features. The ventral pattern of juvenile and immature birds differs from those of adult females which may help to prevent misdirected display—a worthwhile economy under the exacting conditions which prevail.

By far the most highly ritualized behaviour in frigatebirds is the male's sexual-advertising display, or gular-sac presentation. It is homologous throughout the family. Enhanced by its communal nature, gular presentation is extraordinarily conspicuous

and noisy. The bill is pointed skywards and the scarlet sac is couched between the widely spread wings, which vibrate and are rotated so that the silvery undersurfaces are turned upwards. The body shakes and the head is swivelled from side to side. The elongated scapulars are partly raised and the tail cocked. The displaying male vocalizes loudly, claps his mandibles, and may produce non-vocal noises (see 'Voice' above). If a female flies over, the display rises to a frenzy. The female may partly descend, check, and then inspect another part of the colony, or she may hover or circle above the group. This seems clearly investigatory. In the lesser frigatebird it is associated with a special "goose-necked" flight posture (Diamond 1975a). The female holds her wings rather flat and straight or even bent slightly forwards, and vibrates them rapidly. Her tail is spread and switched from side to side and the head and neck stretched forwards and down (See Fig. at end of ch. 5). This 'goose-necking' is recognized by males and used as a cue by reconnoitring males to join those who are 'advertising'. Thus they gain the advantage of displaying where females are already showing interest. Male great frigatebirds do not have the benefit of such a clue and are not comparably mobile; they remain in more fixed display clusters.

Although male frigatebirds usually display in clusters, they may display singly or in twos or threes. On Aldabra the commonest cluster-size was 8–15 (great frigatebird) and in the Galapagos much the same, though I recorded as many as 30. Reville notes that newcomers competed for sites near to 7 or more of their displaying fellows and clusters may persist for many weeks even though the individuals within them change. By long periods of observation from a hide, Reville established that females paid more attention to large clusters and males abandoned those which failed to attract females.

The situation was intriguingly different in the lesser frigatebird. Males showed no preference for large clusters and did not contest sites. They spread themselves more regularly or cruised over the colony seeking 'profitable' areas, recognizable by the presence of 'goose-necking' females.

Magnificent frigatebirds commonly form clusters of 4–8 displaying males (Diamond 1975a). Ascension frigatebirds sometimes displayed so

densely that courting birds dislodged incubating individuals and their eggs (Stonehouse and Stonehouse 1963). Christmas frigatebirds displayed singly or in small, loose groups, usually fewer than 8 (personal observation).

Displaying in clusters is a social phenomenon unrelated to a shortage of display-sites. Displaying males attract others. Reville demonstrated that in the lesser frigatebird (but not in the great) the tendency for males to join a group was related to the amount of preceding bill-clattering per male already present. Thus, intense display attracted more males and kept them there longer. As numbers built up, the frequency of gular-presentation per male increased, so that areas with more males had a higher frequency of gular presentation (per male) than areas with fewer. Since such areas were likely to attract females it would be difficult to disentangle the stimulating effect of her goose-necking from that of being part of an intensely displaying group of males.

Unlike male great frigatebirds, male lessers remained in a cluster only so long as females remained interested. Whereas female lessers 'goose-neck' over an individual displaying male, the female great frigatebird sweeps low over a whole series of groups, setting up a wave of display in her wake. Thus, unlike the lesser, she subjects each male to the same intensity of stimulus.

In all species, when a female settles in response to male display, she typically lands directly in front of him, embraced by his outspread wings. He continues head-waving and vocalizing, bill-clapping and wing-shaking. Gradually the new pair begin mutual head-waving, reaching over each other's neck and down to the twigs in characteristic pelecaniform manner. She calls hoarsely and both birds vibrate their mandibles. In all species, this phase of pair-bonding may flare and die for hours. If she remains for several hours pair-bonding is likely, although even after two days the male may be displaced in which case the pair dissolves and the male displays on another site, and presumably obtains a different female.

Great frigatebirds which form a successful bond spend the first day together on the site, take some flights on the second and (males) begin to collect

nest-material on the third. On the first day the male spent about a quarter of the time displaying to the female, dropping to 10% on the second day. The display loses the main vocal component (the warble) after about a week. New pairs of lesser frigatebirds spent 90% of their first day together, dropping to 50–60% by the third. Bill-clattering was only half as frequent on the second day as on the first day, and was absent by the third day. These are the only species for which such details have been gathered and are interesting examples of the waning process of display as the pair-bond strengthens.

The pattern of female settling determines the eventual distribution of nests, with its ecological correlates such as the relationship between density, synchronization and breeding success. This aspect of breeding biology has been studied only in the great and lesser frigatebirds of Aldabra (Reville 1980). Female great frigatebirds did not settle until many advertising males were present in a cluster and the eventual spatial arrangement of nests was predictable from the preceding arrangement of displaying males. The situation in the lesser was quite different. Even the first few advertising males quickly attracted females, resulting in a much lower ratio of advertising males to nests than was found in the great. The spatial distribution of nests was not predictable and nests were spread more randomly.

Pair-bonding

Great frigatebird pairs began building after about three days' pair-bonding on the site whilst the cluster still contained displaying (unpaired) males. As more males joined, the total number of males in a patch continued to increase until almost all the eventual nests had been built, after which unpaired males began to leave. Since females continued to settle, and pairs to build, over a period of four or more months, there must have been many unpaired males entering and leaving clusters.

As a consequence of females quickly settling in the large clusters of males, subsequent pair-formation and egg-laying was well synchronized. In lesser frigatebirds this was not so. Here, females began to settle when there were only a few displaying males

and instead of filling the different clusters sequentially, they tended to fill them simultaneously, a few settling here and a few there. Consequently egg-laying in each cluster was less synchronized.

Stonehouse and Stonehouse (1963) suspected, I believe wrongly, that in the ground-nesting Ascension frigatebird a pair (not just the male) might go together to a number of different sites before laying. Even after laying, they gained surprising evidence of site-change. Of 24 recognizable birds whose new eggs they removed, three males and one female were, three weeks later, incubating eggs, which they said were not their own, close to their old sites. They did not know whether these four birds had retained their previous partners. This remarkable observation, which has never received due attention, indicates that one member of an egg-losing pair (apparently in three instances the male, and in one the female, though the sex of the actual usurper was not known since the event was not observed) had displaced a neighbour and adopted its egg. If true, it would eventually feed a chick to which it was unrelated. Presumably, also, birds which lost their eggs naturally might behave similarly, hence contributing to the vast and puzzling amount of conspecific interference in frigatebird colonies (Nelson 1967c, 1968, 1976). The simpler interpretation is that the new eggs were replacement layings by new pairings, involving one of the marked individuals whose egg had been removed. Due to the investigators, the colony was much disturbed.

There are challenging aspects of frigatebird social and pair relationships. The combination of a territorial system in which males frequently shift their location before eventually pairing and the tendency for breeding to be disrupted at all stages by conspecific males of unknown status, perhaps including failed breeders, poses many questions. Their pairing system and the adoption of a breeding frequency of once or less in two years, has a number of corollaries, one of which is that frigatebirds, except fortuitously, cannot remain with the same partner in successive breeding attempts and thus forfeit the advantages of a long-lived site and pair-bond.

The period of sexual display is energetically demanding. Great frigatebirds may remain on their

display sites for several days more or less continuously. Lessers usually spend only an hour or two at a time, because they remain in an area only so long as there are 'interested' females. To illustrate the time and energy spent in display: on Aldabra, in 1976, male great frigatebirds advertised on average for 78 days per eventual nest in one patch, and 54 in another. The following year the figures were 91 and 55 days. This does not mean that any one individual advertised for 91 days, but that a site was advertised-on for that period before a nest ensued. However, the bigger the group the more attractive it was for females, and the shorter the period of male display. This was not so for the lesser frigatebird, which could take as few as 26 days of male advertising per eventual nest. However, this species is less productive (see below).

Copulation

Almost all details are for the great frigatebird (Nelson 1968, 1976; Reville 1980). Mating occurs only on the nest-site. It may take place within two hours of the female settling though more usually concentrated in the later stages of pair-bonding when it may occur several times within a few hours. Since new pairs may be disrupted, this seems adaptive. As usual in peleceniforms, copulation is associated with the male gathering nest material, each return accompanied by display, mutual building and, often, more copulation. Despite urgent pilfering of nest material the female may nevertheless leave it unattended at this stage. Copulation has no obvious preliminaries and the male does not grasp the female's head or neck, although he nibbles it. He partly spreads and waves his wings and patters with his feet. The female assumes a hunched horizontal posture. Afterwards the male may perform the advertising display with vocalization. Unguarded females may be subjected to attempted rape by neighbouring males. There is strong circumstantial evidence that occasionally a female great frigatebird with an already-fertilized egg may be displaced from her site and may settle with another advertising male. Thus Reville's observation that fewer than 59 days may elapse between a female settling and the egg hatching leaves (subtracting 55 days' incubation) only four days or less for the male

to have fertilized her, the egg to have developed, and the nest been built—an improbably short time. Copulation ceases when the egg has been laid.

Nest

By selecting the male, the female selects the site also. Males seem not to discriminate between females. There is no flight-circuiting or inspection of alternative sites by the pair. Except for the ground-nesting Ascension frigatebird, males of all species collect twigs by tearing them from bush or tree, sometimes on the wing, or stealing them in flight from red-footed boobies or other frigatebirds. Much energy is expended for trivial reward and nest material may lead to aerial conflict between males. Unguarded nests are quickly plundered. Male lesser frigatebirds will fight over a vacant platform, and if the usurping male attracts a female, other males may land nearby, provoking a *mêlée* which endangers incubating neighbours. Female great frigatebirds may collect nest material; one landed on a male's platform whilst he was present and took a twig to another male 10 m away. Most building is by the female in the week or two after pair-formation but additions continue until the egg has hatched. Twigs are positioned with a simple side-to-side head movement holding one end. The nest may be a flat frail platform, loosely woven and endangering the egg at change-over or, more rarely, a substantial structure. Later, the chick's excreta cements it into a durable pad although often the chick ends up perching on a twig with no nest. Pads may be selected as sites by new pairs whilst their previous occupants are still returning to feed their fledged juvenile. One can readily understand why earlier observers thought that the juvenile belonged to the newly courting pair, which they assumed had stayed together and begun a new cycle.

Egg/clutch

Frigatebirds always lay one egg, which is comparatively large, comprising a higher proportion of female weight (up to 5.7%) than a single egg of any other pelecaniform except Abbott's booby. The egg is white, smooth, and thin-shelled, lacking the chalky deposit of pelican, cormorant, and sulid eggs.



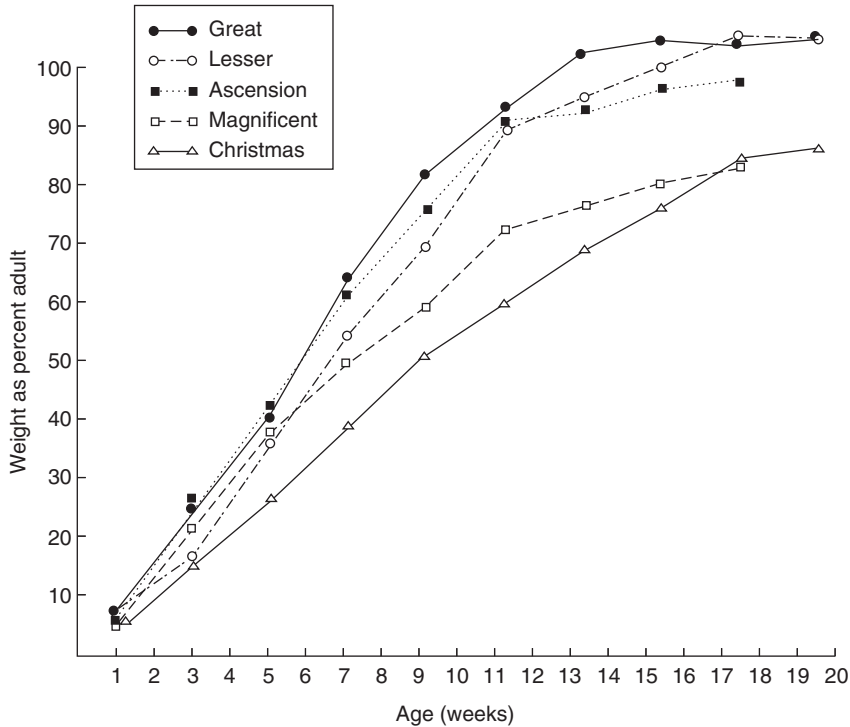
5.39 Frigatebird chick 5-6 weeks. The black 'cape' is characteristic of all frigatebirds. Unattended chick of this age are vulnerable to attack from intruding adult males.

Replacement laying

Although apparent replacement laying has been reported (e.g. Stonehouse and Stonehouse 1963 for Ascension frigate), there is still no proof that it could not be the result of a take-over by another pair, or female. Frigatebird colonies are subject to wholesale conspecific interference, mainly from adult-plumaged males presumably attempting to usurp an established nest. This causes heavy loss of eggs and small chicks, and releases adults which are in incubating condition and may conceivably take over another bird's egg.

Incubation

Frigatebirds and tropicbirds are the only pelecaniforms that do not use their webs for incubation,



5.40 Comparative growth of frigatebirds as percent of adult weight (male/female average).

and since they lack a brood patch, heat has to be transmitted through the abdominal feathers. Both sexes incubate about equally, shifts varying within and between species, the longest lasting more than a fortnight. Perhaps the commonest cause of egg-loss is interference by unpaired males, and Reville noted that, during an apparent food-shortage when many unpaired male great frigatebirds left the colony, not a single incubating pair lost their egg, whereas previously loss had been substantial. On occasion, eggs littered the ground in my Galapagos study-colony and this certainly was not caused by disturbance since we were alone on the island.

During nest-relief the incomer utters the landing call and alights near the nest which is usually quickly vacated, the outgoing partner usually flying off almost immediately. Relieved males may return with nest material.

Incubation period ranges between about 42 days (lesser frigatebird), 44 (Ascension frigate) to 55 (greater), with other species near the latter. Stints

vary with species and region between about 4 and 15 days; probable average 7–10 days.

Chick

Naked, helpless, but not blind, the hatchling strongly resembles a newborn pelican. The scrubby white down grows slowly and after three or four weeks the black scapulars, which have grown disproportionately rapidly, form a cape which may function as a sun-shield in their highly exposed position. An identical shield develops in the canopy-nesting, equally slow-growing, Abbott's booby chick.

Frigatebirds grow more slowly (Figures 3.16 and 5.40) than any other tropical or sub-tropical seabird, perhaps reflecting the adult's highly specialized feeding technique and its offshore foraging. Six months to achieve a modest weight is a long time and foreshadows an equally prolonged post-fledging dependency.

Care of young

Newly hatched frigatebirds are naked, helpless, and unable to thermoregulate. They are closely brooded for about two weeks during which the adults change-over every day or two—much more frequently than during incubation. They are then guarded for a further 1–3 weeks, sometimes longer depending on feeding conditions. Following disturbance small chicks may be cannibalized by conspecifics, including immatures; larger, though still defenceless, chicks may be dislodged. Well-grown young can repel attacks. After about 6 weeks they may be left unattended, even at night, the truncated guard period presumably enforced by the need for parents to forage simultaneously.

Chicks are fed by incomplete regurgitation, very small young up to four times a day in Aldabran great frigatebirds, then every day or two. Gibson-Hill's (1947) report that the Christmas frigatebird dribbles food into the chick's mouth remains unconfirmed. It would not be unique within the Order (see Pelicans, Tropicbirds). Large young may go a week or more between feeds. Males may feed young slightly less often than females. This foreshadows the position in the magnificent frigatebird in which males cease feeding young altogether after about nine weeks (Diamond 1975a; Coello *et al.* 1977). Young are dependent on their parents for considerably more than a year.

Behaviour of young

Begging

Large young beg in a restrained manner by head-bobbing from a hunched position, with drooping, outstretched wings, accompanied by grating and squealing calls. Even when literally starving they do not vigorously assault adults as most young boobies, pelicans, and some cormorants do. Restraint may be an anti-falling adaptation since they can easily become fatally entangled.

Resting, sleeping, and thermoregulation

Chicks rest either upright, prone, or sometimes with drooping head. They may be left unattended when still small, although covered with short, scrubby down

and with a small cape of black, precociously elongated scapulars. They attempt to control body temperature by fluttering the gular skin and panting, but their vestigial webs are useless as surfaces from which evaporative cooling of excreta could occur (cf. some sulids). The black cape may help to control heat loss at night or may protect internal organs from UV rays. Unlike most peleceniforms, young frigatebirds are unable to leave the nest before they can fly properly.

Reactions to neighbours

Nest-defence—lunging, and snapping—appears at about eight weeks. It does not involve ritualized territorial behaviour.

Crèching

Not usual, but young of the ground-nesting Ascension frigatebird may gather loosely though not in 'proper' crèches.

Fledging

In most cases trial flights are not an option and young frigatebirds must wait for full flight before leaving the nest at the age of about six months. There are no observations on the very first flight. The six-month fledging period is exceptionally long and, within the Order, equalled only by Abbott's booby.

Post-fledging

Free-flying but dependent juveniles spend time at sea near the colony or, mostly, resting in the vicinity of the nest. They chase other seabirds and practise feeding techniques. This dependency period exceeds that of any other seabird, lasting from around 6 months to (possibly) 9–14 months (Schreiber and Schreiber 1984) although, lacking observations on marked individuals, the extreme figure is debatable. Despite this, in the Galapagos (1964) many free-flying juveniles starved when parents stopped feeding them (Nelson 1968). As previously mentioned, this protracted dependency added to the long fledging period, prevents frigatebirds from breeding successfully more than once every two years at most (the male magnificent frigatebird is a partial exception).

Because of this unusual breeding cycle, coupled with the male's trait of moving his display site until he attracts a female, frigatebirds cannot maintain a site or mate for successive breeding attempts.

Breeding success

Low hatching success seems common in frigatebirds. In some populations and years it is considerably less than 20% (but the effect of disturbance is never fully known). Since there is often considerable loss of small chicks due to interference and (in some localities and years) of large, even free-flying, young due to starvation, breeding success is mostly low or very low. A generalized figure might be 10–50% of eggs giving rise to fledged (free-flying) young, with enormous regional and year differences. Predation can be locally significant, as on Tower (Galapagos) where short-eared owls take unattended chicks. Productivity among frigatebirds, further reduced by rest years, may thus be uniquely low and longevity great.

Fidelity to colony, site, and mate

Breeding philopatry is likely to be high, natal philopatry perhaps less so but there is no good information. Fidelity to a particular nest-site and mate is impracticable because of the nature of the breeding cycle.

Age at first breeding

Unknown. First breeding could be long deferred, perhaps for up to 10 years. An unusually long period could reflect the frigatebird's specialized feeding behaviour in often impoverished tropical oceans.

Non-breeding years

As mentioned, frigatebird colonies may contain adult-plumaged, non-breeding birds. They may be experienced breeders taking 'rest' years, adult-plumaged pre-breeders or recently failed breeders. Both adult-plumaged and immature frigatebirds may interfere with breeders by attacking and sometimes displacing unattended chicks or harassing incubating birds.

Prior to their appearance as displaying males or prospecting females, the lives of frigatebirds between independence and breeding are little known. They wander widely and may turn up in hundreds on rocks or islands where they never breed.

Longevity and mortality

For populations to remain stable, average lifespan must be at least 25 years and individual spans often substantially longer. Given their low productivity, adult mortality must be extremely low, perhaps no more than about 3% per annum. Mortality rates between independence and first breeding are unknown.

Causes of death

(See Chapter 4.) Natural deaths ensue from starvation in some areas such as the Galapagos; a high proportion of newly independent juveniles starve and ENSO presumably affects frigatebirds. Accidents kill frigatebirds in the breeding colony, e.g. entanglement in branches. Some birds are storm driven. A few must fall to marine predation. Ectoparasite infestations, though probably usually sub-lethal, may be heavy and include flat flies (*Hippoboscidae* sp) and feather mites (*Acarinae*). Internally, the red blood cell parasite, *Haemoproteus*, infected up to half the juvenile population of some Hawaiian islands and nearly a third of adult males (Work and Rameyer 1996).

Tropicbirds

Introduction

Bosunbird derives from the long tail, like a marlin spike, and from its whistle (though only the red-billed actually whistles). 'Tropicbird' describes its preferred latitude and *Phaethon* is variously ascribed to its apparent following of the sun or diving out of it, an allusion to Zeus' slaying of Phaethon, son of Helios the sun-god, with a thunderbolt (del Hoyo *et al.* 1992).

Tropicbirds form the smallest family in the Order. They are the spirits of the tropical, blue-water seas, at home in the furthest ocean reaches

despite their energetic flight, which uses sustained and rapid wing-beats rather than prolonged gliding or soaring. Nor do they appear to rest much on the water. Their breeding biology is dominated by their habit of highly pelagic foraging, often in impoverished, or food-patchy areas, with which is associated, as in other such pelecaniforms, low productivity, slow development and a variable breeding cycle (though Schreiber 1996 gives evidence for dissent).

Classification

(See Chapter 1.) Fossil finds have resulted in taxonomic redefinition at the sub-ordinal or even ordinal level but the three extant species—namely red-billed, red-tailed and white-tailed—are closely related within the single genus *Phaethon*, or possibly even within a single super-species. The validity of the sub-species, usually attributed to the white-tailed and red-tailed, is open to question.

Tropicbirds are unusual among pelecaniforms. They are only moderately colonial, never breeding in large, dense aggregations; their courtship is mainly aerial; they conspicuously lack the extensive repertoire of highly ritualized behaviour found in core pelecaniforms; their calls are tern-like; they nest in holes; their egg is patterned; they do not incubate it on top of, or beneath, their webs; their hatchlings are downy and their young do not feed directly from their parent's throat. Furthermore, several skeletal features are idiosyncratic. Their feather lice are different from the genera found on other pelecaniforms (Zonfrillo personal communication) and they lack their *Pectinopygus* lice. Of all the pelecaniforms they are most likely to be removed from the Order.

The bird

Voice

Tropicbirds, as solitary foragers, are generally silent at sea. Although noisy at the breeding colony they never generate a fraction of the clamour of a pelicanry or a gannetry. Typically, a small group of displaying tropicbirds scream raucously or utter 'kek-kek' or 'ky-ep' calls (white-tailed), cackle, croak or

utter a not-unmusical 'ky-ep' (red-tailed), or more of a whistle (red-billed). Rattles, croaks, and growls have been recorded and intimate calls at the nest-site include a soft 'chuck-chuck'. The sexes seem alike in voice. White-tailed are less vocal than others.

External features and anatomy

Tropicbirds are medium-sized, robust, but streamlined, up to about 50 cm excluding the elongated tail streamers in the centre of the wedge-shaped tail. The streamers, which are highly flexible and may droop, trail or tilt upwards or sideways, are not essential for effective flight; birds manage with broken, abraded, or missing ones. The sharply pointed wings span up to a metre or more. Although the span of the white-tailed approaches 80% of the red-tailed the former weighs only about half as much (extremes of weight *c.* 200 g for the white-tailed, *c.* 1,000 g for the red-tailed).

Tropicbirds possess 11 primaries; the outermost minute and primary 10 longest. There are about 24 secondaries and 12–16 tail-feathers. Streamers, often longer than head and body combined, are stiffer in the red-tailed than in the other two species. They may be stabilizers, visual stimuli in courtship or, on Zahavi's (1975) controversial theory, 'handicaps', the overcoming of which marks out particularly 'fit' individuals.

The predominantly white plumage, which does not vary with season, may be suffused with pink (red-tailed) or, uniquely among seabirds, is a startling apricot yellow in the golden morph of the white-tailed tropicbird, found mainly on Christmas Island (IO). Contrary to some accounts, there is sometimes a difference between the sexes, the male showing stronger colouration (Howell). Both the pink and yellow pigments are probably carotenoids, possibly contained in the oil from the preen gland. Tropicbirds show a variable amount of black, especially as wing-bars but also as an eyestripe. All juveniles show heavy black barring on the back which, particularly in adults of the red-billed, persists as fine black vermiculations. The adult red-tailed appears to have moved furthest away from the juvenile plumage in that it has less black on the wing tips and few, if any, vermiculations.

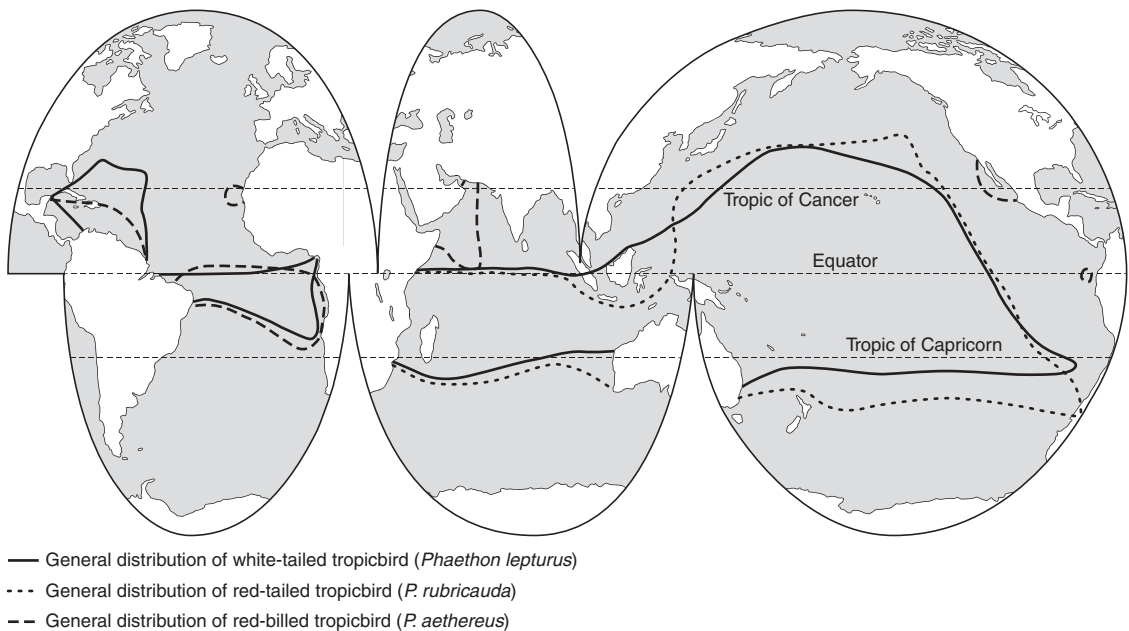
Several authoritative accounts—most prestigiously *Birds of the Western Palearctic* (Cramp and Simmons 1977), and *Handbook of Australian, New Zealand and Antarctic Birds* (Marchant and Higgins 1990)—credit tropicbirds of both sexes with a single, median brood patch but Howell, specifically studying incubation, convincingly asserts that they have none; Schreiber and Schreiber (1993) concur. The egg is tucked beneath the abdomen; the adult may place one or both feet, or neither, on it and the feet make no important contribution, sufficient heat being passed through the ventral feathers. By placing a thermistor thermometer probe in an egg and putting the egg beneath an incubating bird, Howell recorded a consistent incubation temperature of 37°C, some 12°C higher than that of the adjacent shade.

The long, stout and slightly decurved bill is deepest at the base and slightly flattened laterally. It is sharply pointed but not terminally hooked. The cutting edge is finely serrated in adults. The slit-like nostrils are well defined whereas in other pelecaniforms they are occluded. Whereas in core pelecaniforms the os palatinum bone is fused to

the parasphenoid rostrum, in tropicbirds it is not. There is no bare, coloured facial skin and no gular pouch but the bill itself is bright red or yellow. The large, dark eyes impart a misleadingly gentle appearance.

The tropicbird's most striking feature is the small, weak pelvis and hind limbs. By contrast, the pectoral girdle is strong, presumably because the high-aspect ratio wings impose high wing-loading and, since tropicbirds depend on rapid and continuous wingbeats, the flight muscles are large and the pectoral girdle strong and deep-keeled. Long wings result from a long upper-arm bone; the distal part is relatively short. Howell suggests that the long humerus, short forearm, robust pectoral girdle and massive pectoral musculature facilitate the strong, rapid wingbeats needed for hovering, helped by reduction in the weight of the posterior. The value of hovering flight might be in display or positioning for a plunge dive. Tropicbirds possess interconnected, subcutaneous air-sacs on the ventral surface which, as in sulids, cushion the plunge.

The short legs are set back (though not exceptionally so). The small, dull-coloured feet are webbed



5.41 The world distribution of tropicbirds.

between all four toes (the characteristic mainly responsible for their inclusion in the *Pelecaniformes*) and can be of only limited use for propulsion. The middle claw lacks a comb (pecten) but the claws are sharp and strongly curved (effective for scraping and digging).

Locomotion

Tropicbirds are extremely awkward on the ground, shuffling about, using their 'elbows' to hoist themselves forward. Although they prefer to nest on cliffs or slopes, which assist take-off, they will, if necessary, struggle over rough ground and through vegetation or land awkwardly on it and then flop through.

Tropicbird flight is powerful and arrow-like. Their strong, rapid wing-beats resemble the falcon's winnowing flight, though more usually compared to that of a pigeon or tern. Like the falcon, they intersperse glides in level flight. The white-tailed, lighter in proportion to its size, glides more than the other two species and flies more buoyantly. The red-tailed and red-billed appear more laborious. Usually they fly high above the water, alone or in twos. At sea they often rest on the water, floating buoyantly with tail-streamers cocked.

Body maintenance

There are no detailed records of preening, oiling, bathing, and other maintenance activities. Tropicbird plumage is fully waterproof and they can live at sea indefinitely. They seem never to preen thoroughly, using the preen gland, on land (Schreiber and Schreiber 1993).

Moult

Adults undergo complete moult annually (Schreiber and Ashmole 1970; Schreiber and Schreiber 1993). It is largely suspended during breeding. Of 57 red-tailed tropicbirds examined on islands of the Central Pacific none was moulting wing or tail feathers though there was some body moult (King 1974). However, on Christmas Island (PO), primary moult did overlap with breeding to some extent, more at the beginning of the breeding cycle than at the end (Schreiber and Ashmole 1970). On

Aldabra (IO) there was even more overlap; 1.3% of birds on eggs $n = 77$ and 13.9% of those on chicks $n = 36$ were in active moult (Phillips 1987). More than one wave of primary moult can progress at any one time and over a protracted period. The tail streamers, which wear particularly quickly, are replaced constantly, unrelated to the rest of the tail or flight feathers. The moult of flight feathers, in serially descendent order, is staggered, two or more generations coexisting as in other pelecani-forms. Since a complete annual moult means that no wing feather can be more than a year old, tropicbirds differ from (at least) the sulids in this respect. Possibly, tropicbird flight, involving rapid wing-beats for long periods, and their predilection for highly saline seas, is particularly abrasive. Juvenile plumage changes within 15 months, probably starting with a complete moult, to a sub-adult plumage which persists into year two at the end of which adult plumage is present except for traces of immaturity, e.g. in red-billed the central part of the longest secondaries and outermost primaries remain black (Schreiber and Schreiber 1993).

Range and status

The three tropicbirds are often sympatric, but the two larger, red-billed and red-tailed, only in the central Indian Ocean. Unless breeding sites are limiting, as seems possible on Ascension Island, competitive exclusion seems unlikely. They prefer warm, clear, and salty water, between 24 and 30°C and of salinity between 33.5 and 35.0 parts per thousand (Muromtzev 1958). They often occur in far-flung reaches bereft of other seabirds. They range further north of the Equator than south, breeding in Bermuda (white-tailed) and the Azores (red-billed). Of the three species, the red-tailed probably breeds the furthest south. Although mainly occurring to 30°N and S, it strays well beyond these limits (Sp Acc) whereas the other two species rarely venture south of Capricorn. Tropicbirds are characteristic of the tradewind areas of the central and west Pacific and the southern Indian Ocean. The red-billed and white-tailed occur in all three major oceans but the red-tailed is absent from the Atlantic.

Whilst it is not possible to estimate the world population (Sp Acc) the white-tailed is probably the most numerous and the most widely distributed. Especially numerous in the Caribbean, it occurs in good numbers, also, in the Indian Ocean, for example in the Seychelles and on Christmas Island. Probably the least populous is the red-billed, which may have its biggest population in the Galapagos islands. Del Hoyo *et al.* (1992) suggest a world population of fewer than 10,000 pairs for this species. The red-tailed, too, is most numerous in the Pacific though it has greatly declined recently (Sp Acc). There are maybe 5,000–7,000 pairs (de Korte 1991) in the Indian Ocean. In the past, tropicbirds have been heavily persecuted for their plumes, and although no species is currently threatened, present populations are far below natural levels. However, a few populations are apparently stable or even increasing.

Movements

It is unlikely that any species shows true migration though there may be significant transequatorial movement, possibly following the warm, saline conditions which they prefer. Tropicbirds disperse widely, becoming nomadic, pelagic, and solitary wanderers over vast tracts of tropical and sub-tropical ocean. It has been suggested that mates may maintain contact at sea but this is unlikely to be habitual. During 21,000 hours and more than 300,000 km, 87% of all sightings of red-tails in the Pacific were of singles (Gould *et al.* 1974). The average number of 'birds per sighting' was only 1.9 compared with 12.79 for the pelagic sooty tern. They penetrate even into the heart of the barren Sargasso regions and Bennett (1860) recorded several during April at Lat. 23°17' N Long. 42°50' W, about as far as possible from land in the sub-tropical Atlantic (Murphy 1936). However, some populations of white-tailed tropicbirds may remain all year near to breeding localities, presumably their own. Recoveries from more than 15,000 ringed red-tails shows little interchange between islands (Schreiber and Schreiber 1993).

Sightings of juveniles at sea are rare, and of juveniles with an adult rarer still. Ainley *et al.* (1986) saw a juvenile in company with one or two adult

red-tailed on 10 occasions in the South Pacific although never in 29 sightings of red-billed or 26 of white-tailed. Solitary red-tailed juveniles were seen on six occasions. They never saw a juvenile fed at sea. The adult/juvenile groups averaged 544 km from the nearest island. The birds flew within 30 m of each other, calling 'responsively', and stayed together during the period of observation. On two occasions the members of the group sat for many hours on the water within a metre of each other. Nevertheless it seems unlikely that adults accompany their offspring and it still remains to be shown that post-fledging feeding occurs at all. Ainley *et al.* suggest that association at sea may be valuable in transferring information on feeding and foraging techniques.

Foraging and food

Tropicbirds forage during the day, often hundreds of km from their breeding localities although nearer to them during egg-laying and incubation than at other times (Gould *et al.* 1974). During foraging the white-tailed flies at about 47 km/hour (Fuller *et al.* 1988) which agrees closely with Schaffner (1990b). During transects, red-tailed tropicbirds were seen at all hours of day but most commonly in the morning, peaking around 10.00 hrs. Foraging tropicbirds often circle or hover with downward-pointing bill, at a height of up to 50 m. After spotting prey, they drop or dive from a few metres to 50 m (average *c.* 25 m) with half-closed wings, perhaps spiralling or otherwise compensating for the movement of prey. They may smack into the water sending up a fountain of spray, or barely submerge, opening their wings immediately on contact. They can submerge for more than half a minute although often for only a second or two (average *c.* 26 sec). Many emerge tern-like, with fish or squid held crosswise in the bill, before swallowing it. For their size, tropicbirds take remarkably large fish, up to 15–18% of their body weight.

Warheit (1990) points out that tropicbirds show relatively long phalanges which, he suggests, is a trait of wing-propelled plunge-divers. Howell suggests that tropicbirds show convergence with some terns and perhaps fill a feeding niche between that of large

terns, which take surface and sub-surface prey, and the plunge-diving sulids. Among the large terns only the crested ranges widely beyond continental coasts. Coincidentally, tropicbirds, like terns, but alone among pelecaniforms, hatch with downy plumage.

Gould *et al.* suggest that the tropicbird's feeding method, fixing onto a particular item and tracking its movements on the approach dive, may be incompatible with the mêlée of a mixed-species feeding flock and on the few occasions when they do participate they are usually on the fringes. Although gannets and Peruvian boobies track-dive their prey, they can feed amidst a hailstorm of their fellows, but their prey is dense shoaling fish whereas tropicbird prey will usually be more dispersed. Although attracted to vessels, they do not attend them for long and are not found among the offal-squabblers. Like frigatebirds and red-footed boobies, tropicbirds opportunistically take flying fish in the air though Schreiber and Schreiber (1993) say this is rare. Apart from a substantial difference between the white-tailed and the two larger species in the size of prey items (Diamond 1974), there are no qualitative differences in foraging and feeding within the genus.

Like other pelagic feeders including the sooty tern, tropicbirds convey their catch in their crop or lower in the alimentary tract, and Diamond (1974) noted that in the red-tailed the bolus delivered to the chick may be thickly coated with mucous which partly protects it from digestion. Regurgitations of white-tailed tropicbirds feeding near to the breeding colony apparently lack such mucous (Dunlop *et al.* 1988).

The prey is mainly flying fish (Exocoetidae) and squid (Ommastrephidae) but also other species of fish and cephalopod up to 25 cm long, large in relation to the bird and reflecting its powerful bill. (For prey species see Sp Acc and Marchant and Higgins 1990). In Hawaii the red-tailed's diet comprised 18% by volume of squid, mean size 82 ± 3 mm, significantly larger than those taken (same locality) by great frigatebirds but roughly the same as those taken by boobies (Harrison *et al.* 1983). Schaffner (1990b) showed that adult white-tailed tropicbirds could carry food payloads considerably heavier than the average weight of a feed delivered to its chick. He suggests strong selection for parents to feed their

chick less often (fewer trips) but to increase the mass of each feed to a limit imposed by the chick's ingestive capacity. In his view, the mean feed-mass reflects a particular 'target payload' that parents try to achieve as quickly as possible on each of their foraging trips. But although parents can often collect plenty of food for their single chick, the pelagic habit almost inevitably creates intermittent 'feast or famine', favouring chicks with slow growth and large accumulations of fat. The wasteful results of two large and nearly simultaneous offerings overtaking the chick's ingestive capacity is another important vagary of the tropical, pelagic habit, which affects all such seabirds. Schreiber (1996) provides important evidence that red-tailed tropicbirds adjust their food-gathering to match the requirements of their chick, both increasing and decreasing supply in response to experimental manipulation of brood. She concludes (*contra* received opinion) that limits on food supply is not the only reason why pelagic seabirds have evolved small clutches.

Kleptoparasitism

They may be victims of frigatebirds but are not known to perpetrate piracy.

Roosting, loafing, and clubs

More information is needed. Being solitary feeders and essentially pelagic when not at the nest it is likely that they roost singly when at sea. Off-duty breeders may roost within the nest-cavity. There seems to be a notable dearth of immature-plumaged birds at colonies and no loafers or clubs. However, at some colonies there appear to be many adult-plumaged non-breeders and perhaps some failed breeders, which, as in frigates and masked boobies, sometimes interfere with breeding pairs (e.g. Stonehouse 1962; Snow 1965; Harris 1969).

Habitat and breeding biology

Habitat

The family's predilection for warm, saline, and often impoverished oceans has already been emphasized. On their oceanic breeding islands they use a wider

variety of habitat than their specialized anatomy might suggest. They nest in cavities or under protuberances on cliffs and slopes; they use ledges, excavate beneath boulders, penetrate vegetation on flat atolls and, on Christmas Island (IO) even nest in holes or branch-crotches beneath the canopy, far from the sea. As in numbers and distribution, so too in catholicity of site, the white-tailed excels. But tropicbirds prefer cavities in cliffs or slopes, which facilitate landing and departure and provide shade, and there is often fierce competition, both within and between species, for optimal sites (Stonehouse 1962; Snow 1965). Cover is highly desirable, for tropicbirds lack the bare gular skin which can dissipate heat, and their small webs are ineffective for evaporative cooling. When heat-stressed they gape and pant and may desert their egg.

Colonies

As pelagic foragers, tropicbirds might be expected to form large colonies but existing ones are small or moderate. Nor are they dense. Many pairs nest in semi-isolation and groups tend to be loose. This may be because hole-sites are not numerous. Semi-continuous activity around tropicbird colonies results from the presence of non-breeders and from the nine or ten-month cycle, which means there are always some pairs coming into breeding condition. Also, many of the pairs which lose egg or chick soon begin a new cycle (Sp Acc).

Frequency, timing, and duration of breeding

All tropicbird species lay in every month of the year, though often with peaks and troughs. The two larger species have an approx. annual cycle and are unlikely anywhere to breed successfully more than once a year, but the white-tailed tropicbird's successful cycle (interval between successive, successful layings) averaged only nine or ten months on Ascension (Sp Acc). On Tower, Galapagos, laying peaks in the red-billed tropicbird (as, also, in the red-footed booby) occurred when food was most available. Thus Harris (1969) observed

periods of apparent shortage during which many young died of starvation or fledged prematurely whilst simultaneously both breeding and displaying birds deserted the colony and no new eggs were laid. But on Plaza, in the same archipelago and during the same period, all was well. The difference in the timing of breeding on the closely neighbouring islands of Plaza and Daphne—in the first case scattered through the year, and in the second markedly seasonal—may have been due to strong intraspecific competition for sites on the former, but Harris's observation raises the possibility that each colony has its specific feeding areas, which may not be productive at the same time. Earlier, Brosset (1963) noted dead young on Daphne and Tower, which he thought had been deserted by their parents. ENSO events may terminate or delay breeding; for example on Christmas Island (PO) fewer red-tailed tropicbirds attempt to breed, nesting is delayed by 3–6 weeks, more young die, and chicks grow more slowly (Schreiber and Schreiber 1993).

The time required to incubate the egg and rear the chick is about 17 weeks in the white-tailed, 18 in the red-billed, and 19 in the red-tailed but there is much variation between individuals and areas. To these figures must be added the time, roughly up to two months, required to establish or re-establish a site and pair-bond.

Territorial behaviour

Between breeding cycles (length 21–7 weeks) tropicbirds disperse to sea. Nevertheless, because of a-seasonal breeding there are always tropicbirds at the colony. Phillips (1987) notes that white-tailed tropicbirds on Cousin Island (Seychelles) occupied nest-sites a month or two before laying though visits were brief and irregular at first, becoming increasingly frequent and longer up to mating, which was often recorded the first time the partners were seen together. This implies that one partner, perhaps usually the male, returns to a previously used site and awaits the return of a known partner. Site-and-mate fidelity, common in tropicbirds, would facilitate this. In the case of first-time breeders or bereaved individuals the continuous breeding regime ensures that

there are usually potential partners present at the colony. In red-tailed tropicbirds the re-occupation of a site by a particular pair may be episodic and prolonged, lasting up to three months, and gradually leading to longer and more frequent visits, thus fitting more easily into a pelagic foraging habit than would near-continuous occupation.

Tropicbirds have no ritualized territorial (site-ownership) display but often fight vigorously during contests for a nest-site. They interlock bills and stab and slash, causing gashes around the eyes and mouth and (rarely) death. Tropicbirds locked in a fight may remain silent and motionless for long periods although red-tails emit guttural screams. Contestants twist each other into contorted positions using wings as levers. During threat, they raise folded wings, retract the head (which they enlarge by ruffling the feathers), and spread and raise the tail. They head-shake and screech, the vocalization often betraying an otherwise concealed bird. No ritualized threat or appeasement has been described.

Although, as mentioned, they can use a variety of sub-optimal sites they are predominantly hole or cavity-nesters, scarcity of which may lead to considerable strife. On Bosun Bird Island (Ascension), one tenth of all sites were occupied alternately by red-billed and white-tailed tropicbirds and nearly every site changed hands, leading to much nesting failure (Stonehouse 1962). On Cousin Island (Seychelles), by contrast, most white-tailed tropicbird sites were occupied over a fairly long period, by only one pair, and several sites, previously used, remained vacant for years (Phillips 1987). Ascension is one of the few places where red-billed and white-tailed tropicbirds nest side by side but many localities share red-tailed and white-tailed. On Christmas Island (IO) white-tailed avoid competition by taking to the rain forest of the interior, a highly dangerous environment, whilst red-tails commandeer holes in the sea-cliffs. On Daphne (Galapagos) there is marked intra-specific strife among red-billed tropicbirds (Snow 1965) and breeding success is correspondingly low (Sp Acc). New pairs constantly take over breeding-sites and there is little site-retention between successive breeding attempts. Many pairs utilized sites which Snow classified as

'barely suitable'. By contrast, on the nearby islet of Plaza, there was less competition and many unoccupied holes, though Harris (1969) nevertheless described competition as 'significant'. Breeding success was higher than on Daphne. Harris suggests that red-billed tropicbirds in the Galapagos compete for the best sites even where sites in general appear to be plentiful.

On Aldabra competition between red-tailed and white-tailed (Phillips 1987) seemed much less intense than between red-billed and white-tailed on Ascension. The red-tailed occupied larger cavities than its congener and often nested on the surface, beneath vegetation. Out of 48 sites laid in by red-tailed, 42 were 'open' and only 6 'enclosed', whereas there was only one 'open' out of 25 white-tailed sites. The red-tail's willingness to use open sites meant that plenty were available and very few were used by both species. Even so, red-tails often tried to dislodge conspecifics. These intruders may have been non-breeders rather than 'intending' breeders. If so, they were 'interferers' rather than competitors. However, on Cousin, Phillips estimated that more than a quarter of all chick-losses in white-tailed tropicbirds could have been due to intra-specific competition for nest-sites, though he could not rule out the possibility of 'interference'.

Open sites may be sub-optimal. Low success in red-tails in some abnormal years on Aldabra may be due to exposure of the young to overheating. Even in the white-tailed, the few eggs which failed to hatch were on exposed sites. Shade is a priority; tropicbirds cannot dissipate heat by gular fluttering. Still, other (non-pelecaniform) species lacking gular-fluttering can withstand intense insolation.

Pair-formation

Tropicbirds are the only pelecaniforms lacking face-to-face display. Like that of terns, tropicbird courtship, whose function is to *form* the pair-bond rather than to reinforce an existing bond, is mainly aerial. Unlike terns, however, tropicbirds lack ground courtship, presumably because they are too awkward though in any case their hole-sites largely preclude such display. Aerial display (See Fig. at end of ch. 5) occurs above the sea near the colony and

over land, involving up to 20 birds flying in large gyrations at variable height (up to c. 100 m) and involving different kinds of wing-beat, long downward glides and switching of tail streamers. Flight may be normal but slow, or hovering, and glides are stiff-winged.

Red-billed tropicbirds are said to hold the wings lower than red-tailed in the downward glide, whilst white-tailed apparently lack the upwards-and-backwards flutter present in the red-tailed and glide less frequently, though no detailed comparison has yet been made. Often, red-billed tropicbirds present on the cliffs of Ascension (Stonehouse 1962) launched out and joined in until 10–12 birds were flying back and forth. The flight usually ended with one bird flying into a nest-cavity where it was joined by one or more of the others. These observations imply that flights included already-paired birds as well as potential partners and may be a prelude to re-occupying a site as well as prospecting for a new one.

Aerial display appears to be unconnected with proclaiming ownership of a site or with site-owning status. It seems primarily sexual in motivation and 'advertising' in function. Communal display may serve to attract peers to the group and to synchronize sub-group breeding. But until marked individuals are followed for substantial periods the functional details will remain obscure.

Fleet (1974) claims that only red-tailed tropicbirds without nest and egg perform aerial courtship. In some cases a pair subsequently landed and prospected for a nest-site. However, in all three tropicbirds, aerial display was commonest *after* peak egg-laying (Diamond 1975b). Confusion may result from display by non-breeders who evict breeders from holes without themselves occupying them. Frequently, on Aldabra, members of aerial display groups of red-tails descended to an occupied site and tried to dislodge the occupant. In the absence of the owner, such behaviour can easily cause the loss of egg or chick. Indeed, prospecting birds seem especially attracted to occupied sites (Diamond 1975b). In the red-billed tropicbird, too, such attempted usurpations can lead to loss of eggs or young. *A priori*, aerial courtship seems unlikely to involve egg-owning pairs and more

likely to be performed by pre-breeders or birds which will not then proceed to breed.

For further details of aerial display see red-tailed tropicbird Sp Acc.

Pair-bonding

Tropicbirds lack ritualized pair behaviour at the site and are not known to practise courtship feeding. Mutual preening is likely to occur but there are no details. Little or no nest-material is gathered and the pair do not arrange symbolic material. When they meet at the site, preparatory to changing-over on egg or chick (which they do quickly), they have no meeting ceremony. They are thus notably deficient in structured interactions at the site. Nevertheless, pair-bonds are more durable than in other pelecaniforms except some sulids and often, perhaps usually, persist for two or more successive breeding attempts.

Copulation

Mating, for which there are very few observations, takes place at the nest-site and is not preceded by display or by obvious soliciting. It is brief in (at least) the white-tailed (Stonehouse 1962) and occurs in the hole, the male mounting with extended wings pressed against the cavity walls. The tail is depressed to either side of the female's. Afterwards both birds may swoop down to the sea and return some hours later. Extra-pair copulations and mate-guarding have not been recorded.

Nest

The nest-site is a mere scrape, a few centimetres deep, dug out (mainly by the male) with the sharp claws using backward kicking, after loosening the substrate with the bill. Tropicbirds do not bring nest material to the site but will pick up adventitious material such as stones, twigs, grass etc. and place it on the rim, sometimes accumulating a fair nest. Unlike, for example, some boobies which make symbolic nests, tropicbirds show no ritualized nest-building movements.

Egg/clutch

The invariable single egg is comparatively large, at >8% female weight, similar to the frigatebird's or Abbott's booby. It possesses more yolk than most other pelecaniform eggs (Chapter 3) as an adaptation to provide the hatchling with a reserve against food shortage.

Replacement laying

Common.

Incubation

On Ascension the female white-tailed was rarely on the nest for more than a few hours before laying, thus minimizing depletion of energy reserves, although she may be seen at the colony as much as five weeks before. After egg-laying, partners share incubation but spend little time together at the nest. There are no records of off-duty birds resting or congregating nearby. Although females may incubate for several days immediately after laying, the male white-tailed usually takes the first long shift (more than 36 hours), sometimes taking over even before the egg is dry. Because of the first long stint, males sit for slightly more than half the incubation period—out of 237 observations on Ascension, males were incubating on 56% of occasions, and on Cousin, for 58% of the total time (Phillips 1987). Stints tend to equalize as incubation proceeds. Stint-lengths vary with locality but are always long enough (up to an extreme 13 days) to allow protracted foraging (for the white-tailed, 3–4 days on Ascension, 3–6+ on Aldabra, and 7.5–8.5 on Cousin). Usually there is little room for much physical movement at change-over but calling and mutual billing may occur before the relieved bird flies out to sea.

Howell and Bartholemew (1969) and Howell note that, despite the absence of a brood patch, an incubation temperature of c. 97°F is achieved at the interface between abdominal feathers and egg (which is tucked into them). The bill is used to position the egg and much the same tucking movement is used to retrieve a displaced egg. Howell provides evidence that tropicbirds recognize their own, individually coloured, egg, but discrimination does not

always occur. Egg retrieval is well developed. Incubating birds sit closely, mostly sleeping, but vigorously defending against intruders. Tropicbirds flying past evoke a guttural 'chuck' (white-tailed) or a prolonged scream (red-tailed). Nevertheless, white-tails on Ascension often left eggs unattended for half a day or more, presumably so that the incubating bird could forage, and similar behaviour was noted for the red-tailed (Schreiber and Schreiber 1993). They returned with fresh fish in the crop (Stonehouse 1962) or having increased in weight (Schreiber and Schreiber 1993). Apart from possible intrusion, some exposed eggs could overheat and several of the white-tailed failed to hatch. Similarly, 7.5% of failed eggs on Cousin were in nests directly exposed to the sun, mostly in casuarina buttresses (Phillips 1987). A high proportion of total egg-losses were due to desertion by heat-stressed adults. Birds incubating on open sites gaped, panted, and ruffled their body feathers. The lack of bare gular skin for heat control suggests that tropicbirds are ill-adapted to open sites.

The incubation period is considerably longer than any pelican or cormorant and reflects the tropical, pelagic foraging environment and the precocial hatchling. It varies from 40–5 days, but is usually 42–4.

Chick

The hatchling, covered with long, dense down, is much more advanced than others of the Order and can withstand a long interval before its first feed. Although its growth is slow, it attains approximately adult weight when about half-grown at six-to-eight weeks and may subsequently reach 110% of adult weight although it loses this extra weight before it fledges at about 70 days (white-tailed) or 80–5 days (red-tailed and red-billed). All juvenile tropicbirds are white below and heavily barred black-and-white above. They lack tail-streamers.

Care of young

Either parent may be present when the chick emerges (eggshell pushed out or trampled) and feeding may begin within the hour or be deferred for one or two days. As hatchlings are much better developed than other pelecaniforms they can accept

sizeable pieces of solid food during their first day. Their down enables them to thermo-regulate better than other pelecaniforms, releasing both adults for simultaneous foraging, which can be important in a tropical, pelagic seabird. Generally, new chicks are closely brooded but some white-tailed chicks, at least, are left unguarded for short periods during their first day and by day 4 or 5 parental visits may be restricted to one or two short periods each day. This applied even to chicks which were exposed to the sun. But on Cousin they were attended at night until, on average, 12 days old and for red-tails until 18–22 days. Parental visits become shorter until, by about week 4 (white-tailed) the feeding visit lasted less than 10 minutes. By the time of maximum demand, this species on Ascension was unattended on 97% of observer visits. Nocturnal visits do occur though they may be rare. The red-billed tropicbird on Ascension attended its chick more than the white-tailed, up to 70 days, after which attendance fell rapidly. It appears that tropicbirds cease to feed their young about a week before it fledges; possibly the young cease to beg. Some 'starvation' before departure may facilitate its crucial first flight, though fat reserves must also be important and presumably could be monitored only by the young bird itself.

Behaviour of young

Begging

The way in which tropicbird chicks feed differs from that of other pelecaniforms. The chick's gaping response is triggered by the adult, who touches the base of its bill. Instead of putting its bill into the adult's mouth the chick takes the adult's bill into its own gape. This procedure is obviously easier for the tiny chick than taking food by reaching into the parent's throat, for the adult is in much greater control. Nidicolous hatchlings of other pelecaniforms sometimes die before mustering the strength and coordination required to take food directly from their parent's throat. At about a week old the tropicbird chick gapes and vocalizes at any adult nearby. Its begging call is a guttural chattering or chirping (white-tailed) or a shrill rattling (red-tailed) to which the adult responds with guttural clicks or clucks. There is no record of the later frenzied begging that characterizes

pelican, booby, and cormorant chicks, nor of the ritualized begging shown by frigates and some sulids.

Resting, sleeping, and thermo-regulation

After a period of continuous brooding the chick is guarded and may be partly covered up to about six weeks. Chicks from open-sites as against hole-sites seek shade, gape, and pant, but lack bare gular skin. They are not known to excrete onto their webs for evaporative cooling.

Reactions to neighbouring chicks and adults

Little has been recorded about the ontogeny of behaviour in young tropicbirds. When large (five weeks or more) they defend themselves against intruders but they appear to lack appeasement behaviour and if the intruder is an adult they may be killed. Young red-billed tropicbirds experimentally placed with another chick were attacked by the occupier and usually by the owning adult, but red-tailed will feed strange young if these are placed in the nest (Schreiber and Schreiber 1993).

Fledging

Young tropicbirds are unusual among pelecaniforms in that they are generally reared in holes and are highly immobile. Most of them probably do not move from their nest-site during development, though Fleet (1974) observed that on Kure Atoll, where red-tailed tropicbirds nest on the ground, the young wandered to the beach a week before fledging, exercised their wings and returned to the scrape, but did not return after they could fly. Most young tropicbirds will not have explored and learned the local topography which may partly account for the fact that they fledge precipitately and irrevocably rather than progressively. In fact it would be impossible for the fledgling white-tailed of Christmas Island (IO) to return, since it nests beneath jungle canopy and has a perilous passage to the sea. They fledge at 67–123 days.

Post-fledging

Young remain unfed for about a week before they fledge though whether they refuse food or are not

offered any is usually unknown. Harris (1969) noted that in the Galapagos, adult red-tailed returned to the now empty hole as though expecting to feed them. Unquestionably, some go to sea on their own, do not return, and achieve the transition to independence unaided. Yet, although it would be unique among pelecaniforms to accompany young to sea, it would be convergent with some terns. Ainley *et al.* (1986) suggest that some populations of red-tailed tropicbirds do feed their fledged young at sea. Of 68 sightings (Central and South Pacific) of one or more red-tailed tropicbirds, 9 or more (account ambiguous) were of a juvenile in company of one or two adults. Adult-juvenile groups av 544 km from nearest island. Groups approached, and later departed from ship, together, flying within 30 m of each other and in same direction with responsive calling. But there are no records of adults feeding young. Possibly these were merely chance associations resulting from the response of certain adults to a juvenile, akin to the same phenomenon in the Atlantic gannet, which does not feed its fledged young. Others, but on circumstantial evidence, suggest that they feed their offspring near the nest for up to 30 days after fledging. This simple but important aspect has not been fully resolved.

Breeding success

Parameters vary widely between localities and in different years (Sp Acc) due to differences in predation and oceanography. Egg-loss can be extensive (more than 50%) partly due to competition for sites. A hatching success of more than about 60% (lower than most other pelecaniforms) is good for any tropicbird species, though red-tails, for example, manage more than 90% in some areas (Sp Acc). Fledging success is moderate; many chicks are lost early in development and a total breeding success (chicks fledged from eggs laid) of 35–50% is all that is normally achieved (but see red-tailed tropicbird Sp Acc for an exception).

Fidelity to colony, site, and mate

After successful breeding tropicbirds often use the same site in subsequent breeding attempts and in

such cases generally reunite with the previous partner. However, in some populations there is considerable turn-over of sites and mates and especially of failed (predominantly first-time) breeders. Given that optimal sites are limited, at least in many areas, fidelity would be adaptive but the heavy failure-rate and the continuous inflow of potential breeders throughout the year must make it difficult to achieve.

Age at first breeding

The tropicbird's lifestyle suggests a lengthy pre-breeding period; red-billed tropicbirds first breed at around five years but breeding at less than two has been noted in the red-tailed (Schreiber and Schreiber 1993).

Non-breeding years

All three species compete for sites, severely in the red-billed tropicbirds of Ascension (Atlantic) (Stonehouse 1962) and Galapagos (Pacific) (Snow 1965; Harris 1969), and adults interfere in the breeding activities of others. Whether interfering birds are non-breeders or pre-breeders is not known, but tropicbird colonies probably contain both.

Longevity and mortality

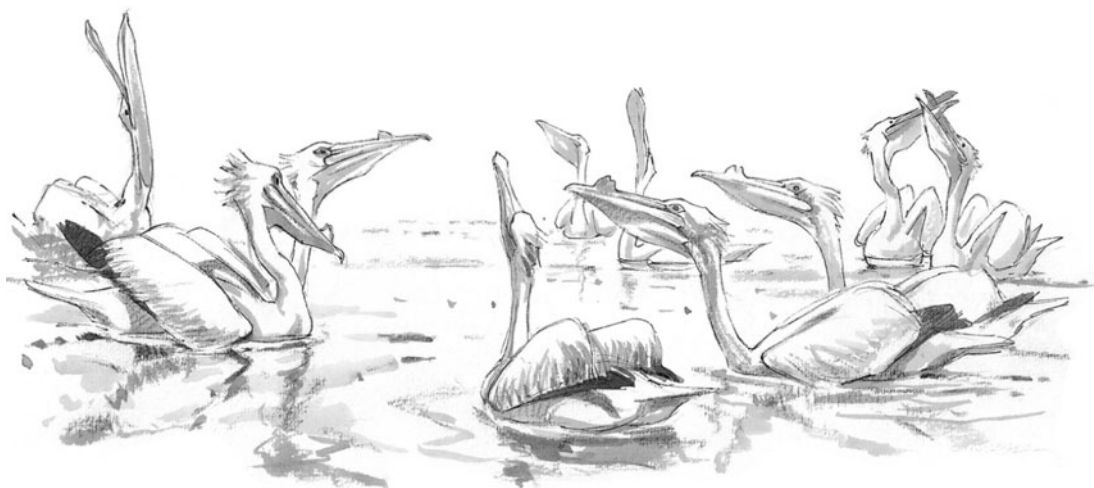
The potential lifespan exceeds 20 years and an annual adult mortality of less than 10% is probable. Figures are difficult to obtain because birds may change nest-sites, take 'rest' years, or lose rings.

Causes of death

(See Chapter 4.) Natural losses include damage or 'grounding' by frigatebirds, storms, predation at sea (several had damaged feet or bill), but the main causes remain unclear.

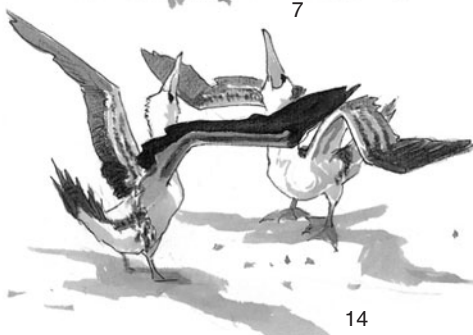
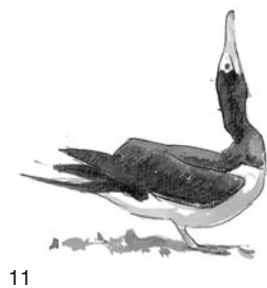
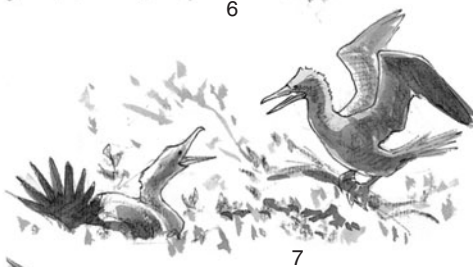
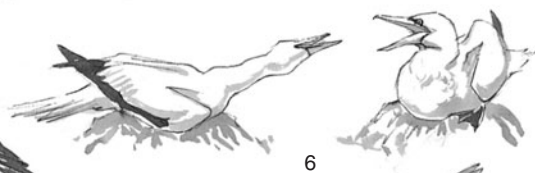
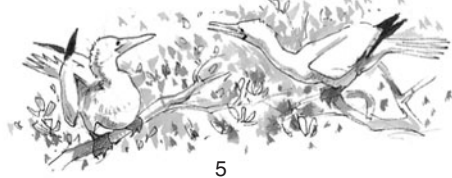
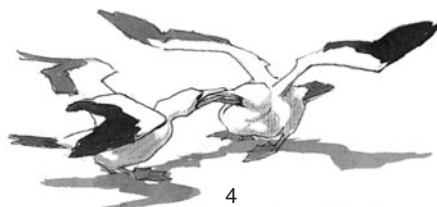
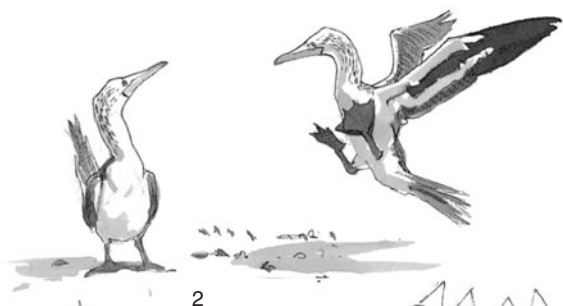
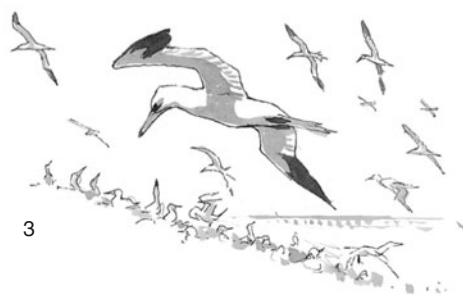
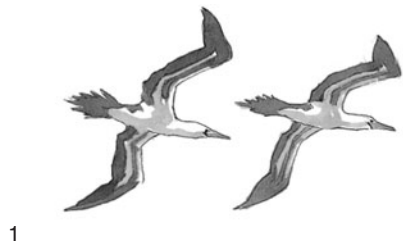
Hole-nesting tropicbirds are less vulnerable than many tropical seabirds. Their colonies are generally small, pairs are often dispersed, and sites inaccessible. Whilst this mitigates the problem of wholesale disturbance or persecution, they still remain highly vulnerable to man and pests, introduced rats and, especially, cats, in many localities.

The following are illustrations of territorial and pair behaviour in the various pelecaniforms; these are referred to intermittently in Chapter 5. All figures by John Busby.



Territorial and pair behaviour in gannets and boobies

1. Ritualised flight-circling (blue-footed booby)
2. Ritualised landing of male blue-foot: 'salute'
3. Colony circling (Atlantic gannet)
4. Overt fighting (masked booby)
5. Unritualised jabbing (red-footed booby)
6. Ritualised threat (Atlantic gannet)
7. Aggressive pair-interaction (red-foot)
8. Ritualised site-ownership: 'bowing' (Atlantic gannet)
9. Site-ownership: Yes/No headshake (masked booby)
10. Ritualised greeting. Contains ritualised aggressive components (Abbott's booby)
11. Male sexual advertising: 'sky-pointing' (brown booby)
12. Male sexual advertising (Atlantic gannet)
13. 'Sky-pointing' in Atlantic gannet has different function in boobies (see text)
14. Mutual sexual display (Peruvian booby)



Territorial and pair behaviour in gannets and boobies

15. Copulation with nape-biting (Atlantic gannet)
16. Copulation, no nape-biting (red-footed booby)
17. Unilateral preening (male to female red-footed booby)
18. Mutual preening (Atlantic gannet)
19. Appeasement: bill-up-face-away (masked booby)
20. Appeasement: nictating membrane drawn across eye nearest to partner cuts-off sight (Abbott's booby)
21. Appeasement: red-foot female turns head away from male, avoiding pointing bill at him
22. Incomplete regurgitation: chick-feeding (Atlantic gannet)
23. Restrained begging by juvenile Abbot's booby (right) as anti-falling adaptation
24. Frenetic begging by juvenile red-foot
25. Gular-fluttering: temperature control (Atlantic gannet)
26. Head-hanging: energy saving behaviour (red-foot chick)



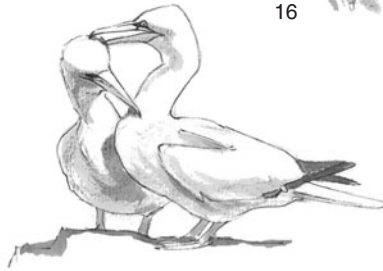
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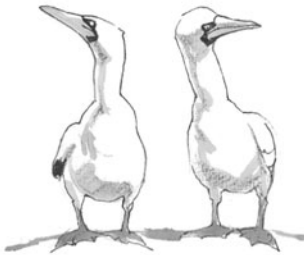
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Territorial and pair behaviour in gannets and boobies

27. Bill-touching (masked booby)
28. Bill-touching (Abbott's booby)
29. Mutual fencing: greeting ceremony (Atlantic gannet)
30. Mutual wing-waving: greeting (Abbott's booby)
31. 'Parading' and 'bill-up-face-away' with 'foot-raising' (blue-footed booby)
32. 'Parading' with 'bill-tucking' (Peruvian booby)
33. Ritualised 'parading' with nest material (masked booby)
34. Mutual nest-building (Atlantic gannet)
35. Ritualised 'showing' of nest material (Abbott's booby)
36. Mutual nest building (red-footed booby)



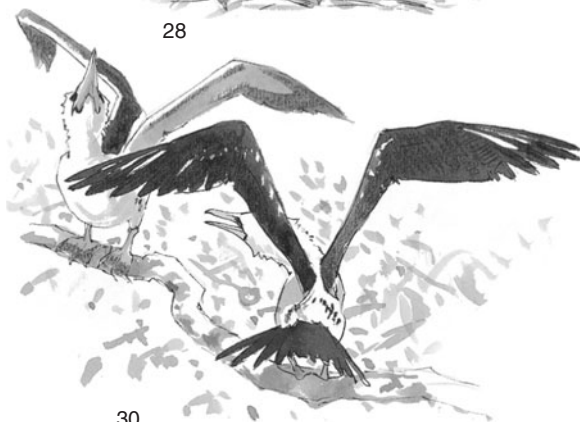
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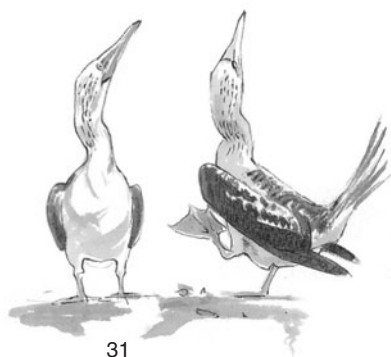
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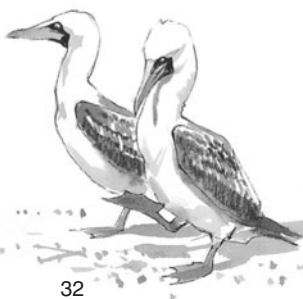
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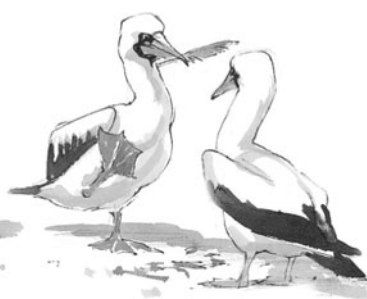
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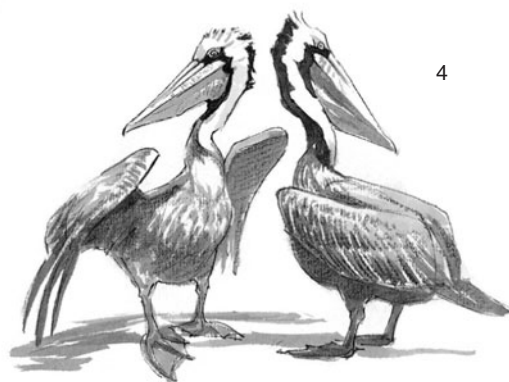
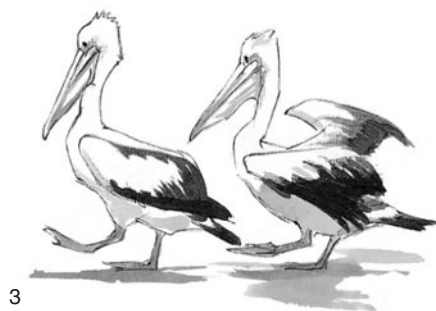
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Territorial and pair behaviour in pelicans

- 1 & 2. 'Headsway' : territorial display (pink-backed pelican)
3. 'Strut-walk' : pair-formation (Australian pelican)
4. 'Head-turning': pair-formation/bonding (brown pelican)
5. Pouch-stretching and eversion
6. Communal display involved in pair-formation (American white pelican)

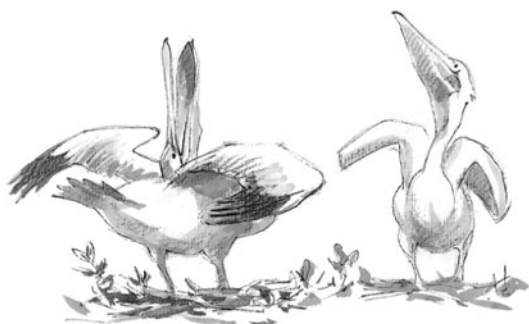


Territorial and pair behaviour in pelicans

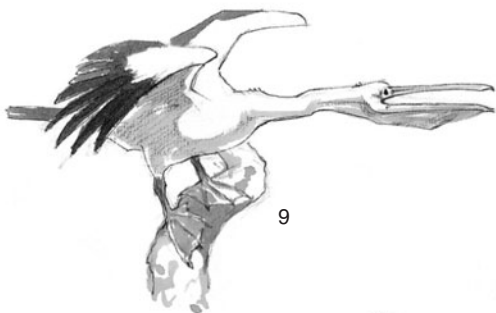
7. Advertising display (pink-backed pelican)
8. Mutual 'head-up': pair bonding
9. Threat
10. Appeasement (Australian pelican)
- 11 & 12. Beak-grappling and aggressive 'head-up' (brown pelican)
13. Communal display: pre-pair-formation (great white pelican)



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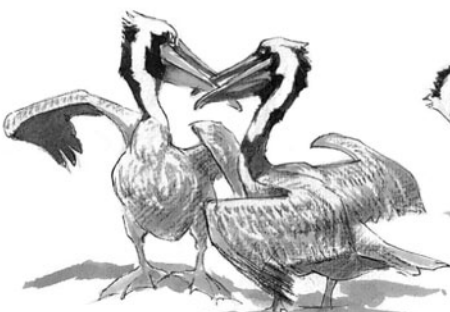
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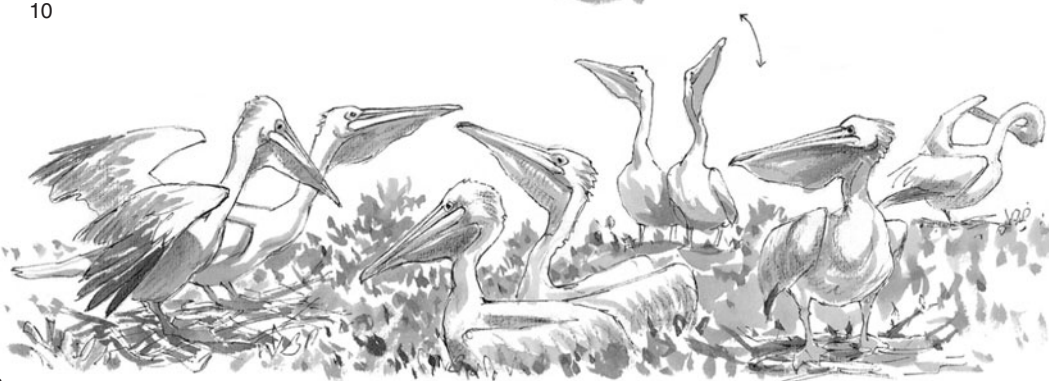
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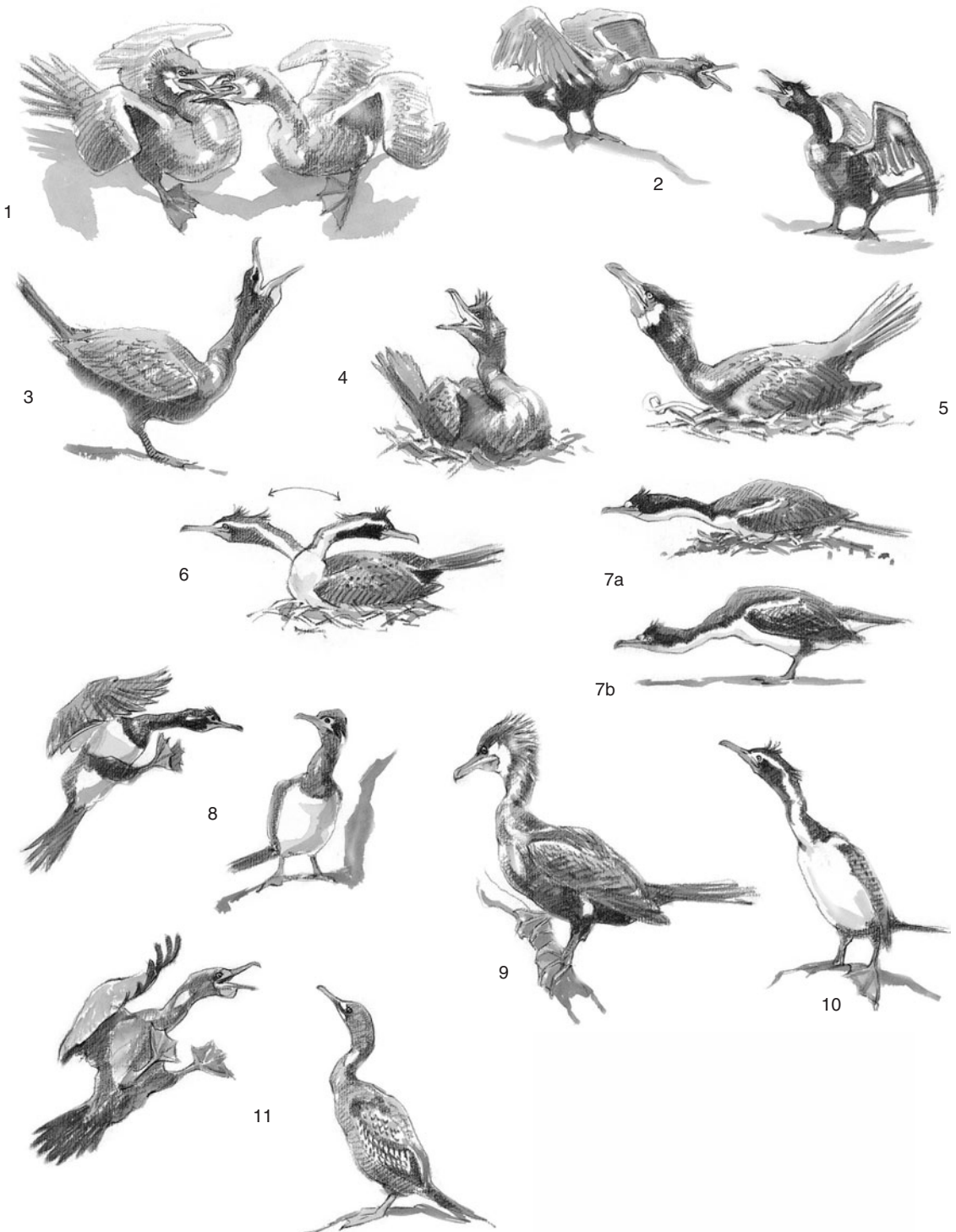
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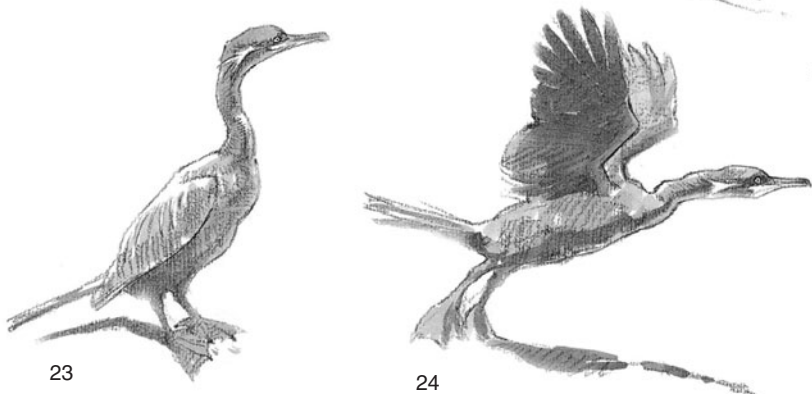
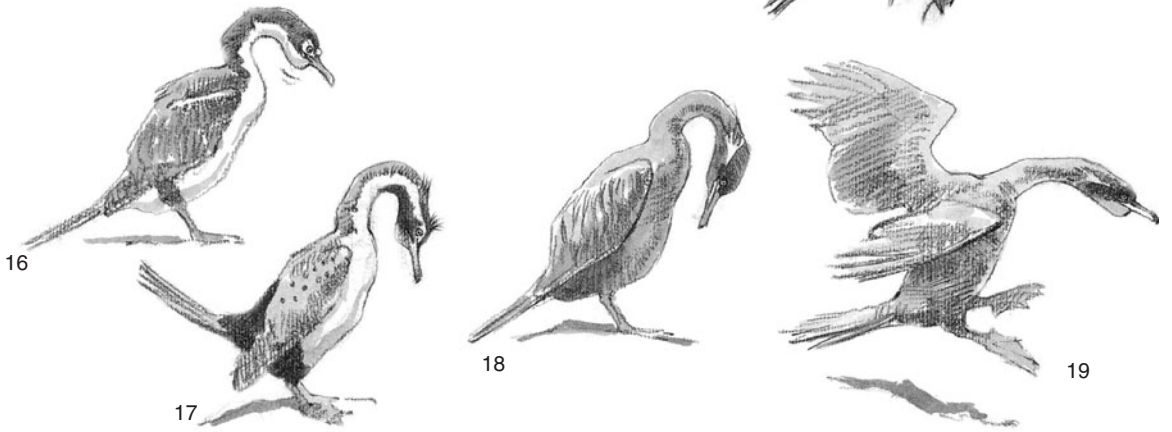
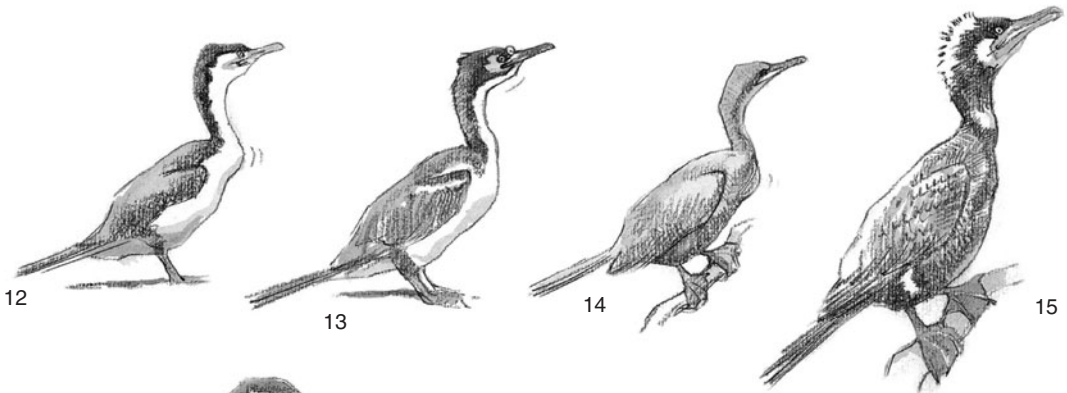
Territorial and pair behaviour in cormorants and shags

1. Overt fighting (great cormorant)
2. Threat (pelagic cormorant)
3. 'Gape display' (double-crested cormorant)
4. 'Gape display' (European Shag)
5. 'Pointing' (great cormorant)
6. 'Swing-pointing' (spotted shag)
- 7a. 'Pointing' (Stewart shag)
- 7b. 'Post-landing' (King shag)
8. 'Ritualised inflying' (Magellanic cormorant)
9. 'Post-landing' (great cormorant)
10. 'Post-landing' (spotted shag)
11. 'Ritualised inflying with kink-throat' (red-legged cormorant)



Territorial and pair behaviour in cormorants and shags

12. 'Pre-take-off' (pied cormorant)
13. 'Pre-take-off' (king shag)
14. 'Pre-take-off' (little black cormorant)
15. 'Pre-take-off' (great cormorant)
16. 'Pre-hop' (king shag)
17. 'Pre-hop' (spotted shag)
18. 'Pre-hop' (Brandt's cormorant)
19. 'Mid-hop' (Brandt's cormorant)
20. 'Pre-hop' (European shag)
21. 'Mid-hop' (European shag)
22. 'Post-hop' (European shag)
23. 'Pre-take-off' (Brandt's cormorant)
24. 'Leap' and 'take-off' (Brandt's cormorant)



Territorial and pair behaviour in cormorants and shags

- 25. 'Wing-flicking' (pelagic cormorant)
- 26. 'Wing-flicking' (great cormorant)
- 27. 'Throwback' (great cormorant)
- 28. 'Wing-flicking' (double-crested cormorant)
- 29. 'Wing-flicking' (little-black cormorant)
- 30. 'Throwback' (little-black cormorant)
- 31. 'Throwback' (Stewart shag)
- 32. 'Throwback' (Megellanic shag)
- 33. 'Head-darting' (European shag)
- 34. 'Throwback' (European shag)
- 35a. 'Wing-flicking' (pied cormorant)
- 35b. 'Throwback' (pied cormorant)
- 35c. 'Forward-swing', follows 'throwback' (pied cormorant)
- 36a. 'Pre-landing 'kink-throat' (double-crested cormorant)
- 36b. Landing with 'kink-throat'



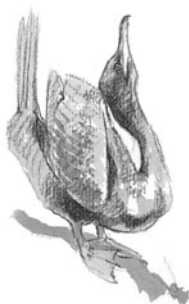
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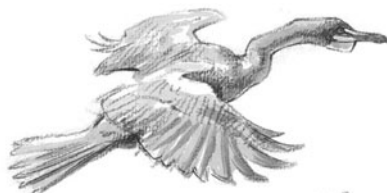
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35c



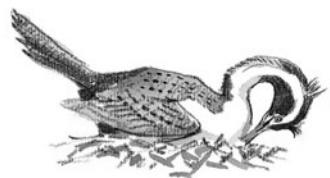
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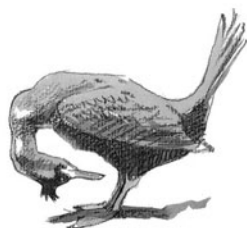
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Territorial and pair behaviour in cormorants and shags

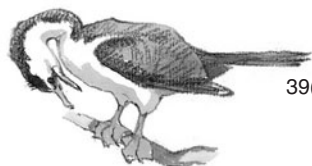
- 37. 'Sitting bow' (spotted shag)
- 38. 'Standing bow' (European shag)
- 39(a),(b). 'Bow' (little pied cormorant-Australia)
- 40. 'Throat-clicking' (European shag ♂ ♀)
- 41. 'Throat-clicking' (greeting) and 'neck-twining' (red-legged cormorant)
- 42. 'Neck-twining' (great cormorant)
- 43. 'Nest-quivering' = 'nest-worrying' (Megellanic shag)
- 44. 'Nest-quivering' (great cormorant)
- 45. Mutual 'nest-quivering' (European shag)
- 46. 'Kink-throat' (Australian darter)
- 47. 'Post-landing' (pied cormorant)
- 48. 'Post-landing' (spotted shag)
- 49. 'Kink-throat' with 'nest-quivering' (double-crested cormorant)



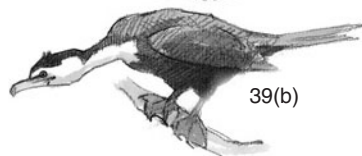
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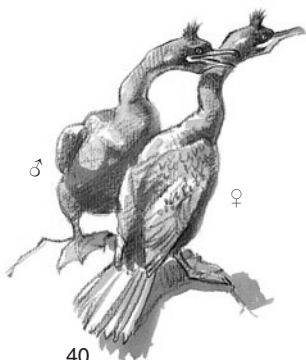
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39(a)



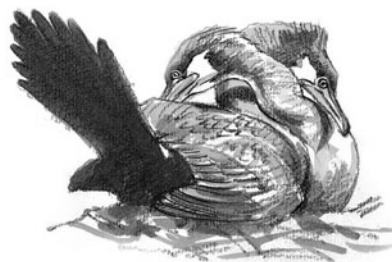
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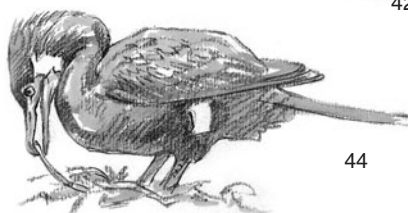
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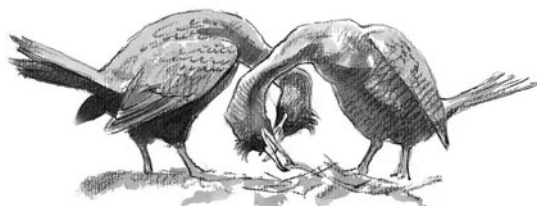
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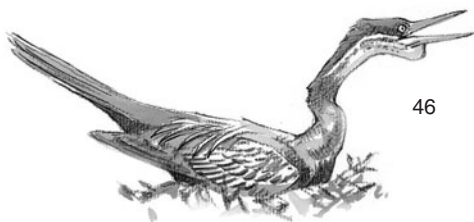
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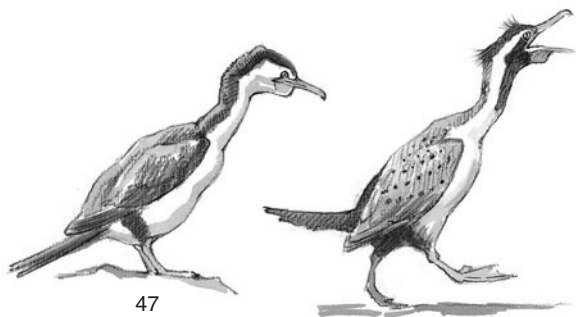
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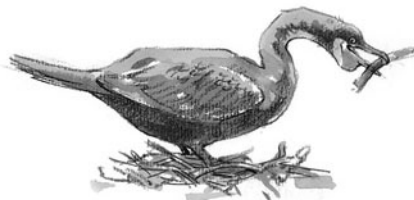


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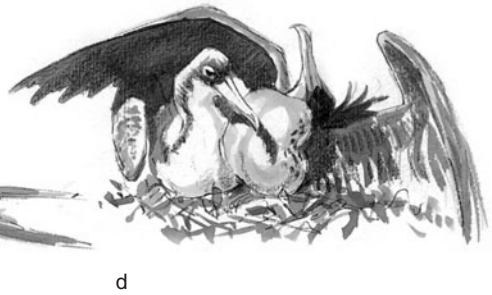
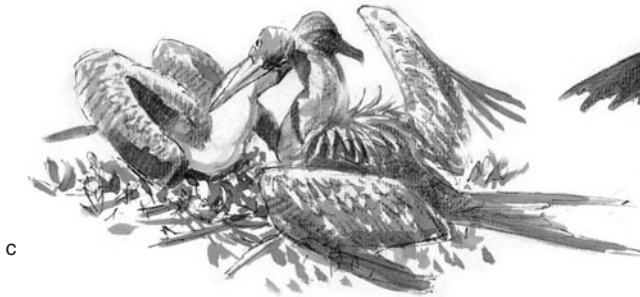
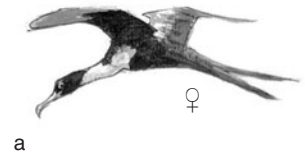
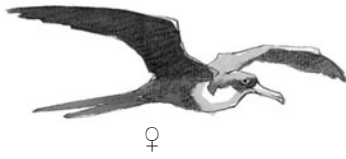


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Territorial and pair behaviour in frigatebirds. (Drawings: J.P. Busby.) (a) Special posture ('goose-necking') of overflying (prospecting) female lesser frigatebird. (b) Group of male great frigatebirds displaying to overlying female. (c)–(e) Simple head wagging and neck-crossing of new pair, great frigatebirds.



Territorial and pair behaviour in tropicbirds. (Drawings: J.P. Busby.) (a) White-tailed tropicbirds fighting over nest-site. (b) Threat. (c) Excavating a site. (d) Overflying nesting area; searching? familiarising?



(continued) Communal aerial courtship red-tailed tropicbird (see text)

PART II

Species accounts

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Pelicans

Great White Pelican *Pelecanus onocrotalus*

PLATE 2

Pelecanus onocrotalus Linnaeus, 1758, Caspian Sea.

Other common names: eastern white, European white, rosy pelican.

French: pélican blanc. German: rosapelikan. Spanish: pelicano vulgar, p. común.

Sub-species

Monotypic. Rosy pelican *P. o. roseus* previously recognized by some authors, including Brown and Urban (1969) but variation in *P. onocrotalus* seems sufficient to account for differences. At Lake Shala, Brown and Urban noted four colour types from almost white with pinkish underparts and virtually no breast patch to dark brown with orange-brown neck, breast and abdomen and even darker breast patch. Upper wing coverts and back grey-brown. Colours apparently acquired during breeding period and rarely seen far from breeding localities. Dark brown birds never described in more northern breeding stations but prevail in most southerly. Whereas pink tinge derived from carotenoid in preen oil, brown, orange and yellow colour due to iron oxide on surface of feathers (Baxter and Urban 1970).

Description

ADULT M PRE-BREEDING: Almost entirely white variably tinged rosy particularly on wing-coverts; some almost red in northern Caspian. Yellowish patch on mid-upper breast, large in some, absent in others. From above, primaries black, secondaries

dark grey shading to whitish with white gap (humeral and tertial) between dark secondaries and body. From below, undersurfaces of primaries and secondaries black. Tail white. Ragged crest (10–14 cm) on nape. White forehead feathers end in point. Pouch, facial skin bright yellow or more pinkish. Long, yellowish bill with red nail; orange, pink or slatey-blue at edges. Swollen orange or yellow knob up to 7 cm high at base of upper mandible appears in most birds prior to courtship. Iris dark red-brown. Legs, feet yellow or more orange.

ADULT F: as M but smaller; crest longer; facial skin and knob orange, not yellow.

POST-NUPTIAL: crest persists through incubation and part of chick-rearing period. Orange-yellow knob disappears soon after egg-laying, becoming wrinkled, flabby, then flat. After post-breeding moult plumage becomes white with pink tinge.

In adult non-breeders facial skin is pink, knob and crest absent.

JUVENILE AND IMMATURE: difficult to distinguish from late-season adult. Mottled brownish above and on head and neck, white rump and ventral surface. Bill grey, eyes brownish, legs, feet pinkish. Immature bird becomes greyer, then whiter; bill turns yellow. Dark centre to hind-neck. Adult plumage acquired 3rd or 4th year.

Field characters

Can be difficult to separate from Dalmatian and pink-backed pelicans at distance but in flight black-and-white pattern on (especially) underwing diagnostic. Separation of immatures difficult.

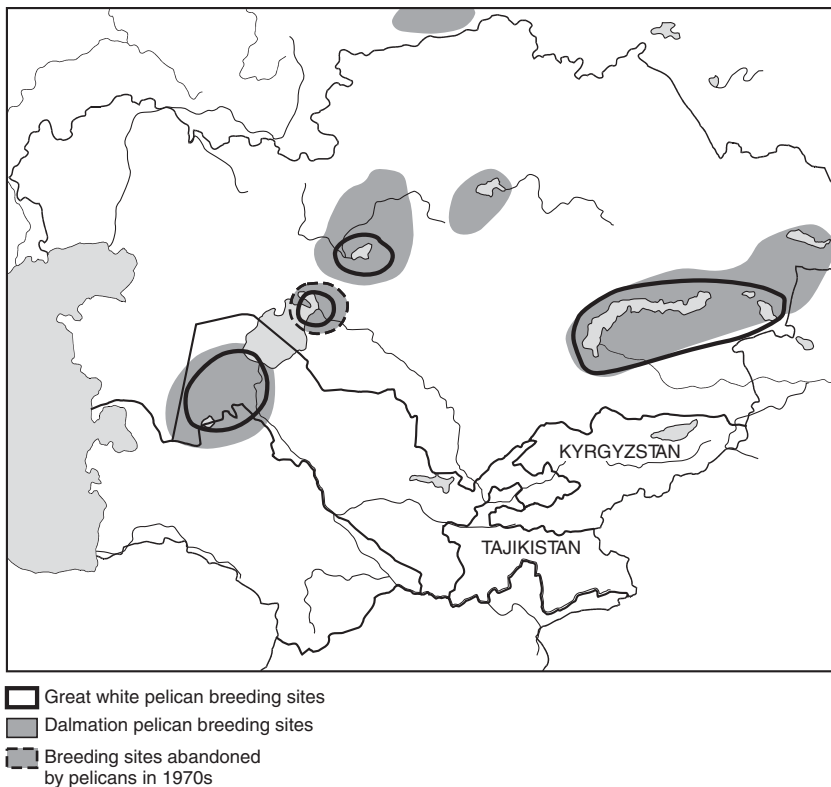
Measurements (see Appendix)

Voice

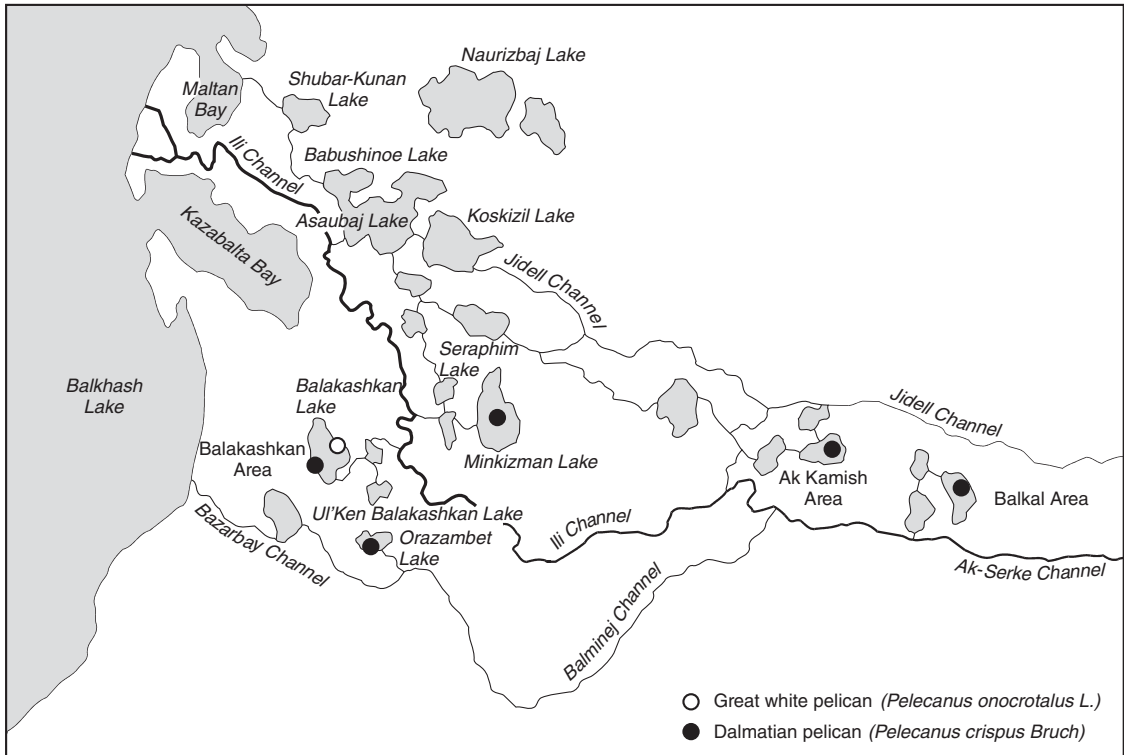
Mainly silent away from colony, at which ‘moos’ (ha-oogh) with closed bill during advertisement (head-up). Nasal grunt (huuh-huuh), growl (oorh-oorh) associated with aggression; rattling growl (rare). Deep croak in flight. Small young yelp; large young utter loud wailing ‘eee-yee-eh’. Large colony emits continuous low-pitched roar, diminishing but not entirely ceasing even at night.

Range and status (Figures 6.1, 6.2)

Two populations; African and Palaearctic. Still most widespread of old-world pelicans from Russia and Danube east to China and south to Natal, although once much more widely spread and numerous; considered by some to be endangered. Crivelli *et al.* (1991a) estimated 7,300–10,500 breeding pairs Palaearctic pelicans in 23–5 sites. Crivelli *et al.* (1994) gives (breeding pairs): Greece 40–100; Iran, 400–800; Iraq, suspected to breed but no details; Pakistan/India, no estimate; Rumania, 3,000–3,500; Turkey, 250–400, 30–50 pairs Karapınar Ovasi, 1985 (Kaegi 1992), up to 35 pairs Gediz delta (Eken 1997); former USSR, 3,100–6,500, total 6,790–11,300 on 10–13 breeding grounds, although this figure could be inaccurate. Probably decreasing in most areas. For



6.1 Past (1970s) and recent distribution of great white and Dalmatian pelicans in Kazakhstan. (From Vinogradov and Auezov 1994.)



6.2 The distribution of great white and Dalmatian pelicans in the Ili Delta, Kazakhstan. (From Zhatkanbaev 1994.)

example, drainage destroyed so much of an important Turkish wetland (Sultansazligo) from 1976 on that pelican population estimated to have decreased by 50–98% by 1990 (Kiziroglu *et al.* 1993). Largest breeding population in Eurasia in delta of Ili river in Kazakhstan where in parts has replaced Dalmatian. In 1987–9 one colony in Balakashkan area held 1,900–2,500 nests. In 1960s and 1970s lakes between Aral Sea and Irgiz River filled up, creating ‘ecological channel’ for pelicans migrating northwards (Vinogradov and Auezov 1994). Then lake Chelkar-Tengiz filled and islands became suitable for nesting pelicans. Finally, large numbers of carp introduced into Irgiz and Turgai Rivers. In 1971 great white appeared in numbers and 300 pairs bred on Lake Chelkar-Tengiz though later lake dried and pelicans left. Eastwards—Lake Balklash and Ili delta—2,400–3,600 pairs bred in 8 colonies in 1970s though numbers dropped after fall in water level. In Europe ‘endangered’, breeding only at Mikri Prespa, Greece.

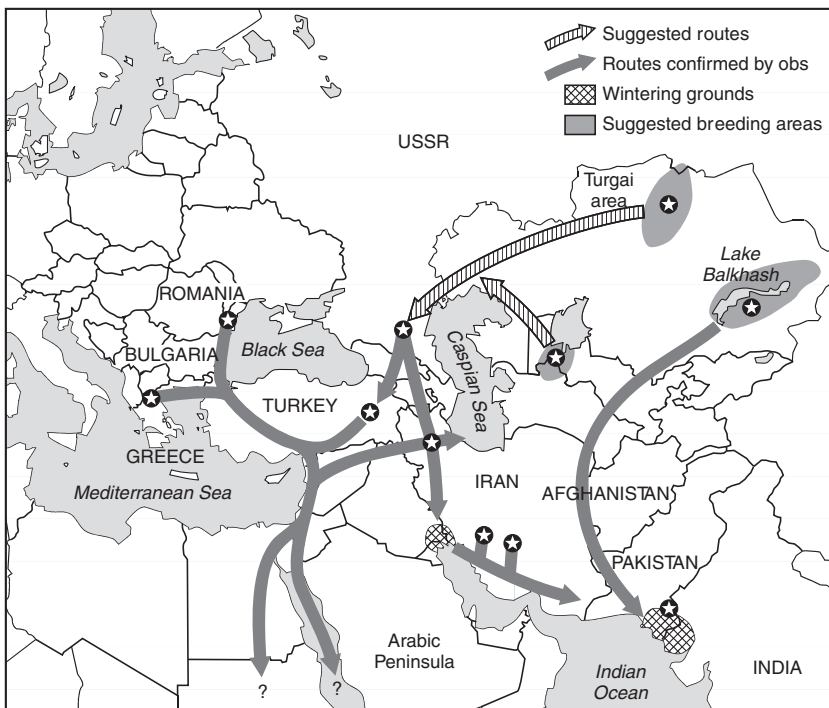
Total African population guessed at 60,000–70,000 pairs (Brown and Urban 1969) or *c.* 75,000 pairs (Crivelli and Schreiber 1984). Crivelli *et al.* (1994) suggest three sub-populations—viz. western (Mauritania, Senegal, Mali); central (Chad, Cameroon) and SE (Djibouti, Ethiopia, Kenya, Tanzania, Zambia, Botswana, Namibia, and South Africa). Western population only recently established but in some years up to 10,000 breeding pairs counted in Senegal. Most of large African colonies near or in Rift Valley. Crivelli and Schreiber point to possible displacement of colonies from Nigeria, Chad and Cameroon to West Africa, especially Senegal and Mauritania. Banc d’Arguin (Mauritania) numbers increased tenfold in 1980s; influx from new colonies in Senegal. Brown and Urban cite, as African breeding localities: Aftout es Sahel; Banc D’Arguin; Lake Shala (Ethiopia); St. Lucia Bay (Natal); Lake Rukwa (Tanzania); Aba Toumour Peaks (Chad); peaks at Kapsikis (northern Cameroons) and peaks at

Wase Rock (Nigeria). Other reported breeding localities are: M'weru Marsh (Zambia); Lake Ngami (old and defunct, in Botswana); Seal Island and Dyers Island (South Africa); Lake Rudolf (Kenya); and Lake Chilwa (Malawi). Note restriction of colonies to islands or peaks. Whilst most colonies traditional and some extremely ancient, opportunistic establishment of large colonies does occur.

MOVEMENTS: each year 70,000–80,000 great white pelicans move out of nesting locality. Birds from SE Europe and Asia migrate to Africa whilst birds from far NE Europe may reach Indian sub-continent. In tropical Africa may move considerable distances from lake to lake although not in predictable directions. Nomadic, seeking feeding localities much as do pelagic seabirds, but overland instead of at sea. Some populations largely sedentary. *Contra* Cramp and Simmons (1977), few wintering records for Red Sea, but regularly occurs there, sometimes reputedly in large numbers. Only 14 from aerial surveys 1992; 1 in 1994 and 1995 (Newton and Symens 1996).

Russian birds depart when frosts begin, between Sept and Nov. Danube breeders depart Sept–Nov though failed breeders, non-breeders and early successful breeders may leave before then. Greek birds depart Aug–Oct.

Migrating pelicans may ascend on thermals to considerable heights and proceed in spectacular numbers and formations. Estimated able to fly av $\approx 1,500$ km without feeding. Examples of migrating numbers in Crivelli *et al.* (1991a): in SE Turkey 7,700, 2 Apr–16 May 1987; in Israel 30,000, 16 Sep–21 Nov 1971, 16,000 1 Apr–6 May 1971, 8,500 20 Mar–23 Apr 1974. Northern Israel a bottleneck and concentrates up to 70,000 during autumn. After taking off, usually ≈ 09.00 – 10.00 hr, ascend in thermals, then glide in parallel V formation 300–1,500 m wide. Can fly at 60–70 km per hour though lose height. As soon as one V-formation finds a new thermal it turns into it and others follow, regaining lost height. Under suitable conditions can glide all day without a single flap. Can average 30–40 km per hour on migration, covering



6.3 Migration and wintering areas of great white pelicans from the Palearctic. (From Crivelli *et al.* 1991a.)

200–300 km per day. Leshem and Yom-Tov (1996), following this pelican by aircraft and radar, recorded av velocity 29.2 km per hour; soaring birds cover 48–91% extra distance from breeding to wintering grounds due to circumventing sea areas and soaring. Fat reserves (av 281 g male, 126 g female) give former theoretical range of 2,500–4,200 km and females 1,100–2,000 km without feeding. En route, feed where can, as at fish ponds in northern Israel, but few or no adequate feeding places. Great whites migrating south through Israel had av reserves of 313.5 g; Shmueli *et al.* (2000) calculated that birds which did not feed in Israel could not fly to their likely wintering areas in southern Sudan. Roost on lakes and wetlands but sometimes on ground, even ploughed fields.

'Stop-overs' during migration are important. Wetlands used by Palaearctic populations during migration and dispersal are: Lake Kerkin (Greece); Lake Kastoria (Greece); Burgos coastal area (Bulgaria); Lake Manyas (Turkey); Lake Huleh (Israel); Bardawil Lagoon (Egypt); Euphrates/Tigris delta (Iraq); Seistan wetlands (Iran/Afghanistan); Indus River delta (Iraq); southern Sudan; Ethiopian wetlands; eastern Saurashtra (India). Many vital sites threatened. Erstwhile important wintering areas in Egypt (Nile delta) drained for agriculture and industry and some Palaearctic pelicans must now winter in Sudan and east-central Africa. More than 125,000 km² temporarily flooded in the Sudd Aug–Nov and may provide good feeding. But no strong influx of birds to swell sedentary pelicans in Kenya and Tanzania Nov–Feb (Crivelli *et al.* 1991a).

Non-breeders seen in flocks in summer in Balkans, Iran, Iraq, and former USSR. Many immatures and sub-adults return to Palaearctic after wintering in tropics and then over-summer until autumn migration. However, majority of birds in first year do not return to natal area. Non-breeders in adult plumage may be present among breeders but immatures are chased by breeding adults.

Crivelli *et al.* (1991a), surprised by large number of observed migrants, calculated number to be expected from known breeding populations in relevant areas. Assuming productivity of 0.9 chicks per pair, age at first-breeding 7 years (surely too high) and 88% of birds breeding by then, figures close to observed ones. Key to large number of birds observed on

migration may thus be large number of non-breeders (1–6 years old) which over-summer in Palaearctic, estimated at 54% of total returning in spring. After two years, immatures cannot be recognized by plumage. Some of these assumptions may be invalid.

Foraging and food

May forage far from colony. Pelicans nesting on Mikri Prespa, Greece, fed elsewhere, including Axios delta (150 km distant) and possibly Lake Kerkin (183 km) (Hatzilacou 1992, 1996). Pyrovetsi (1989) surveyed wetlands to radius of 315 km from Mikri Prespa and found daily travelling distance, one way, of up to 177 km. In Africa forage at least 100 km from colony. Use thermals to ascend and usually depart in groups (2–63 from Mikri Prespa). When foraging in group about 8–10 (range 2–40) swim forward, typically in rough semi-circle, parallel to shore. At intervals and almost simultaneously, birds plunge bills into centre with accompanying wing-flip before swimming on. Estimated success rate 1 in 5 strikes.

Also forages in lines, periodically breaking formation to surround fish. May drive fish into shallows, holding bill open below surface. Feeding may become frenzied, birds milling around and flapping over each other. Saino *et al.* (1995) report that most pelicans on Lake Nakuru fished in synchronized flocks but birds fishing singly attained higher capture rates; these decreased linearly as flock-size increased. Birds in non-synchronized flocks had higher capture rate than in synchronized ones of same size. Nor, circumstantial evidence suggests, were flock-fishers taking larger prey than single fishers. Therefore raises questions about adaptiveness of cooperative fishing. May be useful where prey large, but on Lake Nakuru only abundant prey small *Tilapia*.

Often satisfies needs in 2–3 hours and then loafs. Most morning fishing complete by 08.00–09.00 hr but may feed again in evening. Will also fish at night; on Banc D'Arguin feeds on low or rising tide even at night. In northern Caspian, breeders on nest-duty during day may feed at night. May feed with Dalmatian pelican and great cormorant, each attracting other. May steal from cormorants.

Takes mainly fish. Av daily consumption of captive birds 1 kg (Israel, Shmueli *et al.* 2000). Apparently takes more or less random sizes of fish rather than selecting particular size-range. Prey species

often of no commercial value such as (in Greece) *Alburnus alburnus* which formed main part of chick's diet (Hatzilacou 1992) but in some areas conflicts with fishermen. Hatzilacou (1995) provides details of frequency of chick feeds, food loads and species composition. A 26-day chick received 88.2 g (17.1% of its weight). Fish fry often important; predominant when feeding young. Fry of *Carpio carpio* and *Neogobius* sp important in northern Caspian. Will also take crustacea such as *Palaemon adopus* and *Crangon crangon* and more unlikely items such as cormorant eggs and chicks. Crawford *et al.* (1981) related a decline in small pelican population of coastal Namibia to declining population of Cape cormorant! List of prey in Crivelli *et al.* (1997). Impact on commercial fisheries of Mikri Prespa very slight (Hatzilacou 1996).

Now fewer natural feeding areas, wintering and migrating pelicans favour aquaculture sites (e.g. Israel, Shmueli *et al.* 2000).

Habitat and breeding biology

(See Fig. at end of ch. 5; Brown and Urban 1969; Hatzilacou 1992, 1995; Romashova 1994.)

HABITAT: Mainly inland, often on large areas of water; fresh, saline, or brackish. In Africa, colonial ground-nester; in Europe and Asia, in reed-beds, wet swamps, 'mud' flats, or sand-banks. Despite statements to contrary, does not breed in trees. Off Mauritania breeds on sea-islands; off South Africa on islands and man-made structures; uses islands in river deltas such as Volga and Ural, where nests may be inundated. After floods whole colony may desert and lead nomadic life for summer.

COLONIES: Few, scattered, and sometimes enormous. In Africa especially large, seldom fewer than 2,000 pairs. In parts of former USSR, even today, larger than Europe's remaining colonies, which are usually fewer than 200 pairs. Colonies divided into



6.4 Colony of great white pelicans, Lake Nakuru, Kenya. (Photo: A.K. Kepler.)

number of dense 'units' av \approx 12 nests though (according to author) ranging from 1–54; 9–90; 3–5; 15–20. Distance between units usually 3–5 m though often 10–30 and sometimes 50–70. Between nests variable but \approx 70–80 cm. Laying synchronized within units. When breeding in captivity (first pelican to do so, Rotterdam, 1872) apparently requires group of at least 20 for social stimulation and breeding synchronization (Grummt 1983). Breeding groups form from flocks of pre-breeders. Nests in some localities with Dalmatian pelicans or even cormorants.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually or less frequently if 'rest' years taken but little evidence for this. Nevertheless, proportion of adults which breed every year seems highly variable (Anderson and Gress 1983).

Timing varies with region. In Europe and former USSR strictly seasonal and slightly later than Dalmatian, which often breeds alongside. Arrives Ili delta last 10 days March whilst still thick ice. North of Caucasus arrives Apr, builds end of month and lays until 3rd week May. Balkan eggs laid mainly mid-April–mid-Jun; Greece Apr–Jun. Autumn breeding recorded Ili delta 1989, when \approx 50 pairs began breeding in Aug, downies Sept, flying late Oct. African regime quite different. In Mauritania breeds Sep–Apr, mainly Oct–Jan (dry season); Senegal Dec–Mar; Nigeria Oct–Dec (dry season); Cameroon Sep–Dec (mainly dry); Chad Dec–Jan (dry); Kenya all year but recently mainly in rainy season, peaking Apr–Jun; Tanzania Jun–Sep, when still flooded. Thus mainly prefers dry season but may breed opportunistically during or after rains, suddenly appearing in huge numbers e.g. Lake Natron, up to 30,000 pairs guesstimated. Large African colonies may consist of groups at different stages of breeding. When one departs another may move in, thus leading to continuous breeding. At Lake Shala (Ethiopia) breeding population of 2,500–5,000 pairs (3,000–12,500 pairs 1965–75) comprised groups of 300–1,200, each occupying own area for \approx 90 days. During single year breeding-ground used by 3 or 4 different groups (Brown and Urban 1969).

Failure of adjacent food supply may cause mass abandonment, even in mid-breeding. At Banc d'Arguin, arrival in July coincides with warm water from Gulf of Guinea. Lay in successive waves mainly

Sept–Nov but heavy mortality of chicks of all ages from mid-Dec onwards, mainly Jan–Feb, together with wholesale departure of adults due to cold upwelling. This varies from year to year and drives away main prey, warm-loving, and removes fish from shallows where pelicans feed. Other fish-eaters similarly affected. Also warier than Dalmatian and may desert colony after disturbance or even a storm.

Time between initial occupation of nesting area and egg-laying 13–19 days for March arrivals (Greece) but only 3–5 days for April arrivals. In Russia may be considerably longer if ice slow to melt. Complete cycle, including pre-laying, thus variable but \approx 15–19 weeks.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE GFA: Arrives on breeding-ground in groups. If ice and snow still abounds, sits quietly until temperature rises and then becomes highly active, quickly completing territorial and pair-behaviour. Gathers in groups and mills around. Much communal display between males but females also present in groups, which may splinter such that male displays to male, or male to female, on land or water. Initially, several males may follow one female but eventually pairs form and may then 'parade'. Romashova (1994) describes (for north Caspian birds) remarkable sight of 'several hundred bright pink birds walking in pairs one behind the other, back and forth over a 500–1000 m area'. Once paired, male closely attends female. Ritualized display includes: lunge (threat); 'head-up' (male–male threat and male–female interaction at nest-relief); 'strutting' or parading with female leading; 'bow' (a pair-interaction) and bill-fencing (early courtship). Romashova's account indicates amazing communality and precision of timing: 'straight after feeding on the morning of the day that breeding begins birds fill the chosen site in a dense mass. After calls and quarrels several females sit and begin tucking dry grass underneath themselves. Mating begins in these pairs immediately'.

COPULATION: (GFA)

NEST-BUILDING: Neighbours well within reach, but little friction. Nest-site reputedly selected by female after leading male in ritualised walk.

Grummt (1984) observing captive breeders says male chooses it. Males collect nest-material communally, near to breeding area and with much bickering. Lay heads sideways and scoop into pouch, sometimes amassing so much that hinders movement. Female builds nest, accepting material sometimes with upward jerk of head akin to ritualised 'presentation' of nest-material seen in other peleciforms, especially sulids. Both sexes make nest-scraping or sideways-shovelling movements with bill, head, and neck parallel to ground. Serves to gather material and excavate nest-hollow. Male brings material every few minutes for hours and nest complete in 2–3 days. Steals material, dismantles old nests and even pulls it from beneath neighbours. Can entirely destroy unit of nesting Dalmatians if occupants too few to defend nests.

Nest substantial or mere scrape; loosely lined small twigs and feathers. Base diameter 70–100 cm; cup 30–50 cm; height 30–60 cm. Also recorded as: diameter 34–44 cm; height 3–17 cm or up to 50 cm or 20–50 cm.

EGG/CLUTCH: 94 (80–104) × 59 (52–64) $n = 150$; 92 × 60 $n = 63$ Greece, eggs found outside nest. Weight 155–195 g; 183 $n = 32$, Greece; 162–202 $n = 5$ north of Caucasus (Kazakov *et al.* 1994). Clutch 1–3, usually 2. In Greece, 1984–85, av clutch-size 1.86 and 1.90 respectively. Clutch-size did not decline with laying date (Hatzilacou 1992). On Dassan Island 1.62 (62% held 2 eggs, Cooper 1980); Ethiopia 1.88 (Brown and Urban 1969); Natal 1.89; Banc d'Arguin 1.25 (1–3 eggs per nest) (Brown *et al.* 1982). Clutches of 4 or 5 probably by 2 females. Eggs usually laid 1–2 days apart.

REPLACEMENT LAYING: May occur if first clutch lost within 10 days. Colony may be abandoned after mass egg loss.

INCUBATION: Shared; begins with first egg. Female sits during day, occasionally leaving nest unguarded, and male sits at night whilst female feeds (Romashova 1994). Nest-relief occurs without elaborate display. Incomer approaches, often from in front, in 'head-up' posture with partly open wings. Relieved bird backs off with beating wings and maybe head-up posture. Usually departs within

minutes. Is prone to move off eggs when disturbed. Time from pipping to hatching 24–36 hr. Captive female assisted emergence of chick (Grummt 1984). Incubation period 31.3 days Greece; 33 N Caspian (Romashova 1994); 28–31 captive birds. Other estimates vary widely and probably less accurate. Shifts 24–72 hr, usually 24–48.

CHICK/BROOD: Born naked and helpless with pink skin; eyes open. Day 3 skin slate-grey, later becoming black; said to be already mobile. Day 14 covered with fine, chocolate-brown down which later pales. Day 28–42 down grey-brown, brown feathers erupt on back and wings. Walks well. By day 42 back and wings largely feathered, head, neck, and underparts largely downy, crest visible. Day 42–56 body feathers grow; face, head, and underside become feathered grey-brown with darker wing-coverts and nearly black primaries. Day 56–70 bill dark grey, pouch and bare skin black. No complete growth curve but: at day 9 may weigh 950 g; day 10 1,183; day 11 1,315; day 21 4,000; day 26 5,136; day 27 5,950 (Hatzilacou personal communication). At day 63 may weigh 13,850 g against adult's 10,000. As flying stage approaches young gradually pale overall and pouch yellows. Shortly after first flight young become much whiter and harder to distinguish from adults. Loafs on shore or swims nearby. Later, practises flying, particularly if wind gusty. Fed infrequently.

Brood reduction variable. At Dassan Island obligative siblicide seems usual and only one young reared. Where 2 chicks present both younger than 3 days and smaller showed bruises and blood whilst all dead chicks had extensive head wounds. Nests with chicks 3–14 days held only one alive. Actual attack on sibling observed, even on partly hatched chick. In contrast, Brown *et al.* (1982) say 'brood-losses from sibling aggression apparently slight—only a little desultory pecking observed' and 'surviving broods av 1.5 by day 7 and by day 60 *all* successful adults are feeding single young' (my emphasis). Similarly in Greece, 2nd-hatched chick survived a long time though first dominated over food and grew faster. No instance recorded of two chicks fledging. Yet Appendix 5 of Crivelli (1987) shows 5% nests fledging more than one chick. Seems that age and

method by which one chick succumbs varies with region. (see Discussion of brood reduction.)

CARE OF YOUNG: (GFA) Closely brooded until *c.* 14 days (cannot adequately control body temperature until day *c.* 16, Abraham and Evans 1999). Sheltered and attended more desultorily until *c.* 28 days after which begin to crèche. Adult inverts head so that hatchling can take food from trough near tip, where red nail forms marker or pre-digested food regurgitated into nest hollow (Grummt 1984) though Hatzilacou never saw this. Adults fling away soiled material. Later, colony becomes filthy and trampled, littered with fish remains and dead nestlings. After about a week young given small fish whole from adult's pouch. Medium-sized chicks 'induced' to feed by adult, which shakes them violently by the neck (GFA) but again Hatzilacou never saw this. Nestlings of 250–300 g receive 30–40 g in morning and another *c.* 30 g during day; at day 4–5 receive 60–80 g per feed; 8–10 days *c.* 200–50 g; at week 4 400–500 g per feed and up to 1 kg per day (Romashova 1994). Individual food loads delivered to 7 chicks of known age and weight up to day 28 equalled 3.7–17.1% of their body weight. Max recorded food load 882 g delivered to 26-day-old chick weighing 5136 g. After day 28 food load probably not more than 6.3% of chick's body weight per day (Hatzilacou 1995). At 5–7 days fed *c.* twice a day; from days 7–21 fed about once a day and after this every 2nd day until near fledging, when fed less frequently. Latest age at which known to be fed 97 days. Romashova (1994) experimented with captive chicks. After day 28, if fed large carp (1000–11,000 g) chick refused further food for 'days'. When given fish weighing 600–800 g ate one and accepted another later same day (which oddly, in total weighed more than large carp which satiated them for 'days'). If offered fish of 200–600 g swallowed a total 500–1,500 g and sometimes ate again same day. When offered small fish and fry, ate up to 2,000 g per bout, up to 2,500 g per day. Thus amount eaten depended partly on size of individual prey-items. Interesting implications if true in wild.

Adults forage in different areas at different stages of chick's growth, and timing of feeds during day differs in different months. Apparently match food to stage of chick growth (Hatzilacou 1995). Adults

arrive *en masse* with food for young and relieved birds take off and coalesce into flock which then departs (see American white).

BEHAVIOUR OF YOUNG: Form crèches. Older young join progressively larger pods, up to 100+, and if disturbed readily take to water. Early morning pods smaller than in heat of day when young quite torpid. May move *en masse* during day or even after dark, possibly in relation to wind direction. May sleep in pods. Peregrinations may necessitate parents actively searching for own chick, presumably recognized by appearance, though young also vocalise. After 6 weeks pods disintegrate; young wander freely. Now solicit violently for food; heavy enough to drag adult around. Try to fish (sometimes successful) in groups in vegetated water where *Cyprinus* feed close to surface (Zhatkanbaev 1994a) (cf. Dalmatian which make first feeding attempts singly, foreshadowing adult differences). By week 10 young swim much of time; fish communally, swimming in half-circle and lunging into centre at intervals. These movements instinctive and practised even when little or no food available.

FLEDGING: At *c.* 10 weeks lose weight and practise flying before abruptly departing from colony. Hatzilacou (1995) records juveniles occasionally joining adults in early-morning foraging, but unsuccessfully. Fledging period 11–12 weeks; Ardamatskaya (1994) gives 75 days). In captivity *c.* 100 days, after which young 'detach themselves from parents' (Grummt 1984).

POST-FLEDGING: Grey area. Even as early as 6 weeks, young attempt to fish near colony, and sometimes succeed (Zhatkanbaev 1994a); still receiving food from parents. In northern Caspian late in season, young may be fed on offshore spits, though beginning to support themselves (Romashova 1994). No sustained parental feeding once young can fly competently and leave vicinity of colony. At Mikri Prespa most young feed themselves for 3–5 weeks after fledging and then leave.

BREEDING SUCCESS (Greece, Hatzilacou 1992): Hatched from laid: *c.* 50%. Egg loss due to disappearance (35–8%), displacement (8–15.5%), failure

to hatch (3%), breakage (1.4%). Sub-groups initiated late in season showed higher incidence of eggs disappearing or displaced. Because nests low (cf. Dalmatian) floods may devastate entire colony. Fledged from hatched: 52–4% (66–81% mortality occurred in first 40 days, 30–42% during first week). Fledged per pair: 0.5–0.73. Elsewhere (excluding colony abandonment) 0.8–1.0 young per pair. Usually, authors do not make clear whether mean productivity per successful pair or per breeding-attempted pair. Failure of breeding may be due to desertion (disturbance by man, adverse feeding conditions), predation by large mammals, flooding.

FIDELITY TO COLONY, SITE, AND MATE: Variable, some colonies traditional others opportunistic. Colony-shifts common as conditions change. Even

fidelity to a group within colony weak. Natal philopatry likely to be marked in traditional colonies but little precise information. Fidelity to site and mate probably weak if at all.

AGE OF FIRST BREEDING: Probably not before 3rd year and often not until 4th or 5th; c. 88% breeding by age 7.

NON-BREEDING YEARS: No information.

LONGEVITY AND MORTALITY: Average longevity and annual adult mortality not known but probably can live longer than 10 years suggested by Brown *et al.* (1982). Has lived 46 years in captivity and several were still breeding at 34 (Grummt 1992). Mortality in first year likely to be at least 50%.

Pink-backed Pelican *Pelecanus rufescens*

PLATE 1

Pelecanus rufescens Gmelin, 1789, West Africa.

French: pélican gris, pélican roussâtre. German: rotelpeikan, rotruckenpelikan. Spanish: pelicano rosado.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Overall pale grey; face, throat, underparts whiter; back, rump, underwing washed pink. Primaries blackish, secondaries greyer with silvery edges. Tail whitish with dark shafts. Area of yellowish, lanceolate feathers on breast. Longish and ragged grey crest. Facial skin pink above and yellow below eyes which develop black patch in front, c. 10 times size of eye, and smaller pink patch above it. Eyelids yellow, pouch deep yellow with vertical blackish (some areas light yellow) stripes. Pouch deep red inside. Rather narrow bill pinkish with orange or pink nail. Eye black-brown, red or yellowish. Feet crimson.

ADULT F: As M but with orange eyelids.

POST-NUPTIAL: Pouch becomes greyish or pink with transverse yellow or reddish stripes. Facial skin pale, crest largely lost, black eye-patch less conspicuous. After courtship or during incubation red inside pouch disappears, crest shortens, face and feet lose colour. Plumage greyer.

JUVENILE AND IMMATURE: Mainly brown; head, neck grey; crown tufted. Back, rump, underparts pale grey. Primaries blackish brown, secondaries brown or grey with pale edges. Iris yellow-brown. Pouch pale. Facial skin grey or pinkish; legs, feet grey-pink to yellowish. Later, plumage mottled brown; progressively whitens on back and head. Pouch turns yellow-green, facial skin grey, feet pinkish.

Field characters

Noticeably smaller than great white and greyer, with less black on flight feathers which appear silvery from below. Pink tinge to plumage variable, seasonal and unreliable. Bill uniform yellowish; lacks knob on

forehead; has black smudge in front of eye. Pouch and face pale rather than bright yellow. Feet pinkish rather than yellow of great white.

Measurements (see Appendix)

Moult (GFA)

Protracted but confined to fairly small proportion of flight feathers, especially during breeding when less than 5%.

Voice

Little information; guttural calls at colony, young beg loudly.

Range and status (Figure 5.3)

Largely resident in Africa south of 20°N down to Cape Province. Red Sea (Saudi Arabia, Yemen) to 25°N. Aerial surveys Saudi Arabian Red Sea coast (Jan, Feb 1992–95) recorded 350–600 non-breeders mainly south of 18°30'N. Four major breeding colonies on better-vegetated offshore islands (310 nests, 1995). Saudi population \approx 1,200–1,500 birds and 300–500 on Yemen Red Sea coast. Arabian Red Sea considered of international importance (Newton and Symens 1996). Occurs Senegal and Gambia east to Gulf Aden. Local in western Madagascar but no known breeding since 1960. Common in tropical Africa; breeds Senegal, Gambia, Nigeria, Chad,

Cameroon, Zaire, Kenya, Uganda, Sudan, Malawi, Mozambique, and South Africa where considered endangered. Though patchy throughout range, may be locally abundant in wetlands.

World population quite unknown but not threatened.

MOVEMENTS: Resident, erratic or local movements; vagrants wander more widely, Egypt, Europe, even Britain. No detailed information; picture obscured by escapees.

Foraging and food

Overlaps with great white. Although smaller, sustained flap-glide is still uneconomical and foraging flights use thermals and soaring, though adults seem little delayed on cold, cloudy and wet mornings.

May feed in loose groups of up to 30 but never in fully coordinated manner of great white. More solitary feeder and consequently better able to utilize small patches of water with few fish. Depends on fry and smaller adults from shallows, whereas great white feeds in deeper water further from shore and takes many large, adult fish thus achieving degree of ecological separation. Few differences between two species in duration of trapping, catching, and swallowing but pink-backed 'searches' about 6 times longer before attempting capture and

6.5 The food of great white and pink-backed pelicans in Uganda. (After Din and Eltringham 1974a.)

<i>Fish genera</i>	<i>Frequency (number and % of stomachs in which it occurred)</i>	<i>Av. no. of fish per bird</i>	<i>Av. wt. (g) of fish per bird</i>	<i>Frequency of occurrence, by sex:</i>	
				<i>Male</i>	<i>Female</i>
<i>White pelican</i> (n=65)					
Tilapia	54 (83%)	1.5	503.2	45 (100%)	17 (85%)
Haplochromis	25 (39%)	7.0	67.2	16 (36%)	7 (35%)
Fish fry	8 (12%)	50.2	22.5	2 (4%)	6 (30%)
<i>Pink-backed pelican</i> (n=72)					
Tilapia	32 (44%)	0.8	292.7	11 (100%)	14 (23%)
Haplochromis	16 (22%)	7.0	82.5	1 (9%)	61 (100%)
Fish fry	51 (70%)	576.0	65.8	0	61 (100%)

feeds more frequently. Daily food intake *c.* 776 g or 14% body weight (Din and Eltringham 1974a) but 900–1,200 g (del Hoyo *et al.* 1992). Takes much fry but also fish up to 450 g (mostly 80–290 g); cichlids, especially *Haplochromis* and *Tilapia*, important.

Habitat and breeding biology

(See Fig. at end of ch. 5; Burke and Brown 1970; Brown *et al.* 1982; Din and Eltringham 1974a, 1974b.)

HABITAT: Lakes, rivers, swamps, seasonally flooded land, lagoons, and estuaries but rarely open sea coast. Dislikes steep, vegetated lake margins. Nests in trees, bushes, or reeds but not usually on ground. Reportedly nests on walls of some old African cities such as Kano in Nigeria. Gregarious; often nests alongside maribou and yellow-billed storks, ibises and herons.

COLONIES: Usually contain far fewer than 500 nests. Some used intermittently whilst others endure, even for centuries, often in populated areas and protected; Kasipul (Kenya) used for at least 200 years (Burke and Brown 1970). If trees die, hastened by activities of pelicans, birds move to ones nearby. In Rwenzori Park (Uganda), 6 of 120 trees used in 1967 had fallen by end of season; in 1968, 8 of 150 fell, which must affect continuity of colony (Din and Eltringham 1974b). Single tree may contain many nests; 3 Kenyan fig trees held 250 nests with material intertwining to form communal platform with birds on adjacent nests in physical contact. Occupied trees $n = 994$ contained *av* 2.97 nests (range 1–7).

Colony may include immature birds; at least 100 of various ages, excluding young of year, at Rakewa colony (250+ nests) (Burke and Brown 1970). Often adult-plumaged ‘intruders’ present. Parents repel them but unattended nestlings may be subjected to attempted copulation though apparently not overt attack (cf. boobies, frigatebirds, and tropicbirds).

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually. Timing varies with locality though often in, or partly in, wet season. In western Uganda builds in July, lays mainly Aug and feeds young until Nov; in South Africa lays mainly

Dec–Jan (summer rains); Nigeria lays Aug (peak rains) or Sep–Nov (end of rains) and young fledge in dry season; east Kenya and Tanzania lay May–June (end of rains), young fledging in dry season (details in Johnsgard 1993). Although food presumably more plentiful in wet, perhaps in some areas amount required by pelicans is low relative to local production. In some colonies two or more groups may lay synchronously but separated by period when few pairs lay, and those that do are largely unsuccessful.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Pink-backs perform ‘social advertisement’ soaring flights over breeding area at onset of breeding, which presumably attracts individuals in reproductive condition. Males gather in trees, flying animatedly from place to place and displaying singly or in groups, up to 20 or 30. Sometimes (usually?) these groups contain females. Unusual communal form of ubiquitous ‘head-up’ display in which pelicans suddenly raise their heads and bring bills together in synchronized movement. Similar movements during communal fishing.

Male selects nest-site and during early stages spends all his time there (Grummt 1984 on captives). Territorial aggression may involve overt fighting or bill-grappling (presumably male–male), lunging and threat-gape with wing-thrashing. ‘Pointing’ with extended pouch and open bill, revealing red gape with yellow pouch hanging below, is low-intensity response to intruders, including other species. Often directed at passing pelicans, especially females.

Male ‘advertises’ (sexual) from nest or potential site with ‘beak-clapping’, up to 35 times per min. Head thrown back, bill opened showing red interior, wings raised (not spread) and thrashed, mandibles clapped and perhaps vocalization ‘cho-cho’. Females have lower-intensity version. Several males may advertise to nearby female. Conspicuous ritualized greeting, ‘head-bobbing’, with guttural vocalization, when partners come together. Interactions often involve touching or grasping nest-material, wings ajar, probably displacement activity. May ‘bow’ with pouch extended and bill pointing down and slightly back, a form of bill-tucking; may be appeasing in function. Seems common to all pelicans.

Side-to-side 'head-wagging', head low on shoulders, resembles food-begging of young. Elicited by proximity of another bird but precise context and function unclear. Din and Eltringham suggest 'recognition'—an interaction between partners facilitating proximity and cooperation. However, 'head-bobbing' (above) seems to have more claim to be recognition display.

Courting pairs spend much time together and frequently fly out and return.

Communal 'head-up' display (see above) also occurs in nesting groups, but presumably only where nests extremely close. Function not known and not mentioned by Burke and Brown (1970).

COPULATION: (GFA)

NEST: Takes \approx 1 week; male may bring material 30–50 times per day. Refurbished nests used each year by same pair. Female builds by trampling or pressing twigs into platform. Male may bring material even after eggs laid. Nest usually in trees but sometimes bushes or even among reeds or on ground. Din (1979) found almost all nests, up to 50 m, in tall *Euphorbia* trees. As in brown pelican, nearby perch important for male after he vacates site to female, for relieved partner following pair formation and for both adults whilst feeding large young. Nest made of dead or living twigs becomes solid with droppings but usually collapses during rains or destroyed by other pelicans.

EGG/CLUTCH: Brown *et al.* 1982: $82.1 (72-93) \times 54.6$ ($n = 159$). Weight 119.8 (90–144); 2.4% female weight. Of 155 clutches 128 (82.5%) 2 eggs, 15 (9.8%) 1 egg, 12 (7.7%) 3 eggs; av 1.98. Interval between eggs 2.2 days. First egg laid 48–60 hours after completion of nest (10–12 days after beginning building).

REPLACEMENT LAYING: May occur if first clutch lost early.

INCUBATION: 30 days (33–34) $n = 7$. Stints, both sexes, about 24 hours. Begins with first egg laid usually before midday 48–60 hours after completion of nest. Change-over usually 12.00–15.00 hr, with head-bobbing; sometimes bill-clapping and pointing.

CHICK/BROOD: Hatching takes 20–24 hours. Hatchling brick-red or flesh-pink. Day 8–14 white down appears mainly on back and darkens somewhat, thickening over body except head and upper neck by day 15–21; primaries, secondaries and scapulars erupt. Day 22–8 down thickens and brown primary and secondary coverts appear. Day 29–35 down thickens still more, tail-feathers erupt and primaries well developed. Day 36–42 humerals appear, scapulars fully formed, tail fan develops and short crest appears. Day 43–56 down reduced but still plentiful. All flight feathers present but not fully grown. Wings dark brown but body largely downy and white. Day 57–85 down replaced by contour feathers, wing (black) and tail (brown-black) almost fully developed, wing coverts brown. Head and underparts white. Growth (Figure 3.16) shows sigmoid pattern with inflexions week 2 and 8. Nestling eventually exceeds adult weight by \approx 13% week 10. Brood on hatching averages 1.9; on fledging less than 1.0. Hatching interval of 2 days allows size-discrepancy which, with marked competition for food, favours oldest chick. Smaller sibling frequently attacked and lacerated; withdraws and may be pushed over edge where becomes entangled and dies. Some remain in nest and survive many weeks. Considerable mortality of 2nd chick weeks 3–7, and most of all week 8–9 (Din and Eltringham 1974b). Burke and Brown (1970) recorded highest death rate days 11–30. Despite this prolonged survival, seems no explicit claim that pink-backs ever rear 2 chicks. Clearly some pink-backs waste much parental investment (see Chapter 3, brood reduction). But if older chick falls or is blown down when large, extended insurance policy via younger sibling is valuable.

CARE OF YOUNG: (GFA) Regurgitates partly digested fish or fry into nest when young under 2 weeks. Larger young may take up to 20 min over feed after which adult may rest for half-an-hour before feeding chick from same fish-load. Fully fed young become grossly distended, exceptionally splitting outer skin of neck. At first fed up to 30 times per day declining to 10–25 by week 3, 5–10 during weeks 4–6 and once a day or less thereafter. Frequent feeds do not mean separate foraging trips.

BEHAVIOUR OF YOUNG: Larger young beg by violent head-swaying and wing-beating, pecking parent's bill and sometimes feet—behaviour not recorded in other peleceniforms. Ritualized begging strongly resembles adult courtship. Nestlings 'bow' and 'head-wag', lowering head onto shoulders and moving it from side to side whilst vocalizing. A curious, common and, along with self-biting, uninterpreted behaviour is to tuck bill until tip touches breast and then slowly head-shake. Both before and after feeding chicks suffer violent convulsions (GFA). Until about week 3 sleep in supine position like young cormorants and sulids. Drape head to one side and turn it so that lower mandible faces upwards, wings loosened. Later, sleep with bill resting on neck or tucked into scapulars. Self-preening begins day 3 or 4 whilst sitting and after week 4 whilst standing. Panting and gular-fluttering begin week 3.

Although cannot form pods like ground-nesters, young from closely adjacent nests sometimes group. Large young noisy; groaning and bill-clapping. Young pink-backs that fall out of nest but are still in tree are fed, but grounded young ignored.

FLEDGING: After several weeks leave nest and may be fed elsewhere in tree. Eventually fly well enough to reach trees hundreds of metres from colony and are fed there (cf. brown pelican, which is not fed after it leaves nest). But Din and Eltringham (1974b) report that whilst young do perch in other trees once they can fly, they always return to their natal tree to be fed. Fledging period \approx 12 weeks if defined as capable of sustained flight around nesting locality.

POST-FLEDGING: Fledged young continue to be fed sometimes hundreds of metres from nest tree (Burke and Brown 1970).

BREEDING SUCCESS: Hatched from laid: \approx 90% (Brown *et al.* 1982). Fledged from hatched: $<50\%$; 30% (n = 66, Burke and Brown 1970); 41% (n = 39, Din and Eltringham 1974b). Not more than one chick per brood known to survive to independence. Fledged per pair: 0.95 (Uganda), \approx 0.56 or one juvenile per 3.6 adults (W Kenya) (Brown *et al.* 1982). Mortality, other than sibling competition, due to cold and rain when close-brooding ceases, falling or blown from nest, accident at first flight. No significant losses due to predation or interference by non-breeders.

FIDELITY TO COLONY, SITE, AND MATE: Adults use same colony in successive years but fidelity to precise site and mate not adequately recorded; when fouled trees die, sites have to move. Brown *et al.* (1982) say new pairs probably formed annually.

AGE OF FIRST BREEDING: Definitive plumage and probable first breeding at 3 years.

NON-BREEDING YEARS: No details.

LONGEVITY AND MORTALITY: No direct information but from low productivity and pre-breeding mortality, adult mortality rate of less than 15% per year seems likely.

Spot-billed Pelican *Pelecanus philippensis*

PLATE 1

Pelecanus philippensis Gmelin, 1789, Philippine Islands.

Other common names: grey pelican, rosy pelican, Philippine pelican

French: pélican à bec tacheté. German: graupelikan. Spanish: pelicano oriental.

Sub-species

Monotypic, but formerly confused with Dalmatian, wrongly considered to be conspecific (Delacour and Mayr 1945). Specific name *Pelecanus roseus* was allocated to both, which were then separated as *P. r. roseus* (spot-billed) and *P. r. crispus* (Dalmatian).

But much earlier *roseus* had been applied to a so-called rosy pelican which was, in fact, merely spot-billed. Further confusion later ensued when great white pelican *P. onocrotalus* thought to have 'rosy' sub-species *P. o. roseus* now known to be an artefact (great white varies in size and some birds pink due to pigment in secretion of preen-gland). So spot-billed remains as monotypic species which in two respects (small size and arboreal habit) resembles pink-backed more than large, white, ground-nesting pelicans.

Description

ADULT M PRE-BREEDING: Silver-grey on back with darkish centres to wing-coverts; whiter beneath. Primaries and primary coverts brownish-black, scapulars and secondaries grey-brown; lower back, rump, underwing and under-tail coverts pinkish. Head, neck speckled; untidy-looking. Prominent grey and white (mixed downy) crest or mane. Sclerae around eye bright red. Face mainly orange-yellow with dark patch in front of eye. Bill pinkish with, in early season, bright yellow margin and bluish-spotted sides (hence name) becoming yellowish towards tip, with orange nail. Pairing pelicans have pale bill-tip (Nagulu 1984). Pouch dull purple or reddish. Legs, feet brown or blackish.

ADULT F: Similar; facial skin paler.

POST-NUPTIAL: Crest shed as incubation begins. Eye ring pales. Facial skin whitens. Bill tip becomes bright yellow in incubating and brooding birds (Nagulu 1984). After breeding both sexes browner on head, back; facial skin greyish.

JUVENILE AND IMMATURE: juvenile dark grey-brown with rufous margins to feathers; abrade to more uniform colour. Primaries and secondaries blackish; ventral surface pale. Bill at first pinkish, not distinctly spotted till 2nd year though spots seen before then; purplish spot in front of eye appears late in 1st year. Eye brown, pouch pink, grey or pale bluish; bill similarly nondescript with increasingly yellow nail and terminal edges. Dirty white feet and legs of fledgling darken. Mainly adult plumage by 3 though brown feathers may persist in wing-coverts.

Field characters

Blotched bill and pouch distinguish adult, also combination of black-tipped primaries with pale secondaries and small size distinguish it from Dalmatian.

Measurements (see Appendix)

Voice

Hardly documented; groans, grunts, screeches.

Range and status (Figure 5.3)

Most endangered pelican. World breeding population probably not more than 2,500 pairs and total population fewer than 13,000 individuals. Formerly abundant, though 'millions' in Burma perhaps not literal; widespread in Asia. Now mainly if not entirely in Sri Lanka and SE India though perhaps still present in Burma and possibly other sites in Indo-Malaya. However, not one noted in Burma during Asian waterfowl census (1989–92). Apparently found around lower Changiang river (Fukien) though references in Crivelli and Schreiber (1984) call the Chinese records 'unclear' and may refer to Dalmatian. Occurs, though not known to breed, in Pakistan, Thailand, Laos, and Red River delta in Vietnam. Probably breeds in Cambodia (Mangalaraj *et al.* 1993). Sad decline for more than 50 years attributable to human pressure on feeding and breeding habitats.

In 1981–82 Nagulu and Rao (1983) surveyed known pelecarnies in S. India and found: traditional colony at Telineelapuram held *c.* 65 young and (including these) 200–250 birds; ancient colony of Kundakolam abandoned in 1982 and birds reportedly moved to Ariyakulam; colony at Moondraidapu, some 18 years old, failed to nest in 1982; some nesting in new refuge at Ariyakulam; at Kokkare Bellur ('kokkare' means 'heron') and Bannalli, one of India's oldest pelicanries; three trees used by about 100–150 pelicans, though these authors did not see them. Altogether now no more than 2,000 birds in India. In Sri Lanka, probably main stronghold, may still occur fairly widely. In recent years 23 colonies have held *c.* 900 pairs (Crivelli and Schreiber 1984). Total population perhaps 3,600 individuals. Recent decrease despite theoretical protection in National Parks and Sanctuaries.

MOVEMENTS: Only India, Sri Lanka, and Cambodia harbour reasonable numbers in winter, but knowledge of wintering sites incomplete. World wintering populations (Mangalaraj *et al.* 1993): India 345 (1987), 1,768 (1988), 1,931 (1989), 2,922 (1990), 1,410 (1991) and 2,055 (1992); Sri Lanka 1,092 (1986), 950 (1987), 768 (1988), 3,605 (1989), 1,323 (1990), 3,043 (1991), 905 (1982); Indonesia 6 (1989); Cambodia 200 (1992), 1,252 (1993).

Foraging and food

Little information. Commutes in flocks to and from feeding areas. Departs well after first light. Both solitary and communal feeding observed, latter involving line or semi-circle of birds. Food includes frogs, lizards, and snakes as well as fish.

Habitat and breeding biology

(See Fig. at end of ch. 5; Nagulu 1984.)

HABITAT: Utilizes lakes, rivers, swamps, artificial catchments. Nests (with storks, ibises, herons, cormorants) and roosts gregariously in tall trees often amidst water which may recede. Apparently tamer than most pelicans, remaining undisturbed by noise (even gunfire) and staying on nest until intruder reaches lower branches.

COLONIES: Now comparatively small; scores of pairs may nest contiguously in single tree. In some areas highly traditional, closely associated with human settlement, and protected by locals, though occupation may be erratic from year to year.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually—Oct–May S India; Dec–Mar/April Sri Lanka; Oct–Dec Burma. Cycle takes 24–26 weeks.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Little-studied. On arrival at breeding site takes about a week to settle; no mention of prior communal flights but, later, males do ‘flight-circuit’. No communal display or display on water recorded. Unpaired males settle on tops of nesting trees and perform complex sexual advertising display orientated to prospective partners. With it is mixed

territorial display directed both at potential intruders and, in initial stages, to females. Overt fighting rare or absent but lunges. Points at incomers or overflying predators. ‘Head-swags and bill-claps’ during sexual advertising. Wings held loosely open, tips crossed over tail, and moved up and down. Reddish gular pouch (blood vessels appearing as dark stripes) distended and shaken and bill gapes. Head swung from side to side and swayed up and down, resembling (from front) symbol for infinity. In sexual advertising head-sway usually followed by rapid ‘bill-throw’ which takes head, bill a-gape, over back to tail. Bill-throw followed by 2–4 bill-claps which, at loudest, audible for 300m after which head returns to resting position or head-swaying resumes. Whilst primarily male advertising display, also ‘recognition display’ when partners reunite at nest-site; female’s much less intense than male’s, which in turn weaker than during initial pair-formation. Incoming bird may elicit head-swaying from neighbours and from mate, in which case display acting as agonistic (site-ownership) behaviour. After bout of continuous advertising followed by brief pause, male (and female less intensely) shakes or flutters conspicuous gular pouch. Whilst, under some conditions, gular fluttering thermoregulatory, incorporation into display sequence enhances visual impact of the display.

Initial pair-formation followed by frequent flight circuiting (male) covering 300m around nest tree. Reunion may be followed by head-sway and bill-clap (both partners) and by bowing with neck arched and bill pointing downwards and backwards. In another display performed simultaneously by both partners at nest-site, head is turned slowly from side to side with neck arched. During these displays red gular pouch distended and may be fluttered. Tail, fully spread, moved up and down and from side to side. Occasionally one bird, most often female, passes bill over neck of mate in basic peleciform manner. Partners also cross, and may grasp, each other’s bill.

COPULATION: (GFA)

NEST: Built from low up to 30m in trees. Often contiguous on twiggy, horizontal branches or against trunk, sometimes many in a tree, usually in

groups of 2–5. Alternatively, in vertical forks or even at base of coconut fronds. Never on ground. Utilizes many species including tamarind *Tamarindus*, banyan *Ficus*, illupai *Bassia*, baboob *Acacia*, palmyra *Barringtonia*, mango *Mangifera*, rain-tree *Pithecolobium*?. Building shared but mainly by female from material brought by male. Material brought in bill mainly between 07.00 and 08.00 hr. After that, hot enough to create thermals which can be used to gain height for foraging. Suitable perch ‘relief branch’ important adjunct to nest. Material passed from male to female and since male usually brings tiny amount per trip this may enhance importance of nest-building in pair-bonding. Usually occupies 4–6 days. Nest substantial structure of twigs and branches from a few to 150 cm long, 1–3 cm diameter and up to 550 g. Dry twigs gathered communally from ground rather than wrenched from trees. Even material that has to be pulled is always dry. Pilfering rife, even from beneath sitting bird. Nest lined with grasses, aquatic vegetation, moulted feathers; \approx 50 cm in diameter, 7.5 cm deep cup.

EGG/CLUTCH: $84.4 (73-89) \times 54.6 (45-59)$ $n = 19$; 78.8×53.4 $n = 50$; $71-79 \times 47-54$ Nelapattu pelicanry. Weight: $120 \pm 16.2 (100-145)$ $n = 19$ not necessarily fresh. Clutch, Nelapattu pelicanry— 1.94 $n = 36$ (1980–81); 2.0 $n = 10$ (1981–82). Arredu pelicanry— 3.0 $n = 10$. Commonest clutch-size 3. First egg laid 5–7 days after start of nest-building. Eggs laid 36–48 hours apart.

REPLACEMENT LAYING: Full clutches, if lost, are replaced beginning after about one week. Part-clutches lost are not made up. Presumably clutches near to hatching, if lost, are not replaced?

INCUBATION: Shared; 29–31 days, beginning with first egg. Stints probably \approx 24 hours. Relief mostly once a day 07.00–13.00 hr; brief with head-sway and bow by both or either.

CHICK/BROOD: Hatchling 100–200 g; pale or bright red. White down apparent day 4; chick covered by day 13 at which age it cannot stand but can shuffle on tarsi. Black tips of pre-eruptive primaries visible at 14 days; no trace of tail feathers. Day

17 primaries and secondaries 1–2.5 cm long, wings grey-brown, scapular patches grey but tail feathers still not visible. Day 26 dark grey tail feathers \approx 5 cm long, scapulars dark grey. At about this stage chick demolishes nest. By day 29 chick stands and moves around. Grey-brown contour feathers appear, head and neck mainly white, some grey on head; most of wing grey-brown. Day 35 wing fully grey-brown, scapulars overlap in mid-line. Day 42 head and neck grey (head darker), day 49 grey line whole length of mid-hind-neck, sides and base white. Day 56 grey crest on head. Day 61 wings and tail more or less fully formed. Max weight cited at \approx 30 days but no details; seems very early. Bill and wing probably fully grown 60–90 days. Chicks hatch asynchronously, 1 or 2 days apart. Apparently no obligative brood-reduction. Although Nagulu describes youngest of 3 chicks killed by oldest, middle one remains safe. This surprising discrimination, if real, presumably based on greater size difference between chicks 1 and 3, \approx 4 days apart. Occasionally, 3 young reared. Chicks may fall from nest and, even if well grown, are ignored by adults and die, though reputedly live for some time on fallen scraps.

CARE OF YOUNG: (GFA) Sexes share close-brooding for 10–15 days. In 2 nests 5-day-old naked young died from heat-stress. By day 10 adult moves to rim of nest or to ‘relief branch’ and guard period continues until day 30–35, then unattended. Nest-relief mostly once per day usually between 07.00 and 13.00 hr. If unrelieved, on-duty bird may leave nest for brief period. Relieved birds may depart singly or in company. For first 2 days pre-digested ‘soup’ trickled into mouth of hatchling, presumably from tip of adult’s upper mandible. Between 3 and 13 days chick picks up food regurgitated onto floor of nest (Abbott’s booby is the only other non-pelican pelecaniform to do this). Adults re-ingest spilt food and until day 10 remove soiled material. Up to day \approx 30 chick fed 3–5 times per day but later only once or twice. Food-load 500–2,000 g made up of many small fish or, according to Nagulu a single 2 kg fish! Feeds delivered mainly between 10.00 and 15.00 hr during which period thermals used. Before 10.00 hr birds return at low altitude in extended lines. Adults may land some distance from young (not

clear whether this only after young have left nesting tree). Often, feeds delivered from branch above young. Too importunate young dislodged from adult's pouch by rapid neck-jerking. Entries last from few sec to 6 min. If two young, fed in turn, and after it has withdrawn first-fed never given second feed.

BEHAVIOUR OF YOUNG: Begging vocalizations of larger young ('grunting') accompany violent pestering of adult's bill-tip, pouch, breast, and feet. Chick may head-sway, beat wings, bite twigs or own wings, jerking violently left and right (GFA). At 30–36 days leave nest and dismantle it, thereafter perching on branches until up to 120 days old. But even before 90 days fledglings spend time on nearby water, foraging, bathing, preening, and resting. At this stage congregate closely, as crèche-ing ground nesting species do at an earlier stage.

FLEDGING: No details about first flight or at what age leave nesting tree but well before 90 days since at that age can fly and return.

POST-FLEDGING: Even full-winged and self-feeding young still fed by parents though for how long not stated; may still be present in nest tree at 120 days or fed nearby.

BREEDING SUCCESS: (Nagulu 1984) Hatched from laid: 88.6% (n = 340, 175 nests, 1980–81), 91.9% (n = 594, 297 nests, 1981–82). Fledged from

hatched: 73.5% (n = 250, 1980–81), 73.7% (n = 438, 1981–82). Fledged from laid: 54.1% (1980–81), 54.3% (1981–82); 68% (50 nests, 150 eggs, 102 fledged young, Lamba 1963). These figures remarkably consistent and perhaps indicate pelicans' capability when undisturbed. Much lower figures for ground-nesting species may be partly artefactual. Fledged per pair: just under 2. Failure mainly due to human disturbance leading to predation. Where colony protected, failure may be due to competition between siblings, falling, or extreme climatic factors such as cyclones or excessively high temperatures, especially late in nesting season. Nagulu witnessed deaths of 5 nestlings and an adult during 6 hours in May 1980, when temperature rose to 42°C. Similarly in 1982, temperature in high 30s between 2 and 4 April led to 1, 5 and 15 deaths, all between 13.00 and 15.00 hr. Young birds dropped from trees and were unable to reach receded water.

FIDELITY TO COLONY, SITE, AND MATE: Fidelity to traditional colony probably high. Site and mate fidelity not recorded.

AGE OF FIRST BREEDING: Probably *c.* 3 years.

NON-BREEDING YEARS: No details.

LONGEVITY AND MORTALITY: Potential longevity probably much as other pelicans. Annual adult mortality and causes not documented.

Dalmatian Pelican *Pelecanus crispus*

PLATE 1

Pelecanus crispus Bruch, 1832, Dalmatia.

French: pélican frisé. German: krauskopfelikan. Spanish: pelicano cenudo.

Sub-species

Monotypic. At one time considered sub-species of spot-billed pelican.

Description

ADULT M PRE-BREEDING: Silvery white above, tinged grey-blue on ventral surface Patch of pale yellow on lower foreneck. Ashy on secondaries; black on outer primaries. Undersurfaces of inner primaries slightly dusky and of outer primaries, black. Untidy top-knot of curly feathers on back of head and neck (Russian 'curly pelican'). Eye-ring

purple, iris pale yellow. Bill pale yellow with orange tip, pouch orange-red. Legs, feet lead-grey.

ADULT F: Similar.

POST-NUPTIAL: Pouch pale yellow, other soft parts duller, bill dark greyish. Loses crest. Less yellow on breast.

JUVENILE AND IMMATURE: In first autumn said to be indistinguishable from adults, which are extremely grey due to moult. Upperparts pale brown streaked where centres of feathers darker than edges; underparts dusky white. Head grey-brown, whiter on forehead, bushy crest on crown. Iris off-white. Bill grey, pouch lead-grey to yellow, legs and feet lead grey. Immature becomes whiter, but dingier than adult.

Field characters

Very large; underwing lacks bold black of primaries and secondaries to be seen in great white pelican. Looks white from a distance but spot-billed almost as pale. Pink-backed has blacker wing-tips. Adult lacks any hint of red in plumage. Lead-grey feet

distinctive. Juvenile difficult to separate from spot-billed or pink-backed but larger than latter and range differs from former. Concave line formed by forehead feathers where it meets bill said to distinguish Dalmatian at all stages from great white. Downies white whereas those of great white dark.

Measurements (see Appendix)

Voice

Grunts, groans, hisses, explosive sounds. Greeting call a soft, low 'hch-hch-hch'. During copulation male(?) makes grating call. Alarm call 'wo-wo-wo'. Non-vocal bill-clapping during agonistic encounters. Young grunt and bleat, becoming a 'wa-wa-wa' when excited, especially at feeding.

Range and status (See Figure 5.3.)

Endangered and vulnerable on world scale. Declined at least from late 19th and through 20th Century. Estimate of world population recently reviewed because of information from former USSR. Past and present distribution in Crivelli *et al.* (1994). Breeds exclusively in Palaearctic and now thought to number 3,215–4,280 breeding pairs at 20 or 21 sites (each 'site' can contain several

6.6 Population estimates for the Dalmatian pelican. (Data from Crivelli *et al.* 1994.)

Country	Number of breeding pairs	Number of breeding localities	Comment
Albania	40–70	1	
Bulgaria	70–90	1	
China	?	?	Could be important
Greece	190–260	2	
Iran	5–10	1	
Iraq	?	?	
Mongolia	30–50	1	
Rumania	70–150	1	
Turkey	100–150	4 or 5	
Former USSR	2,700–3,500	8	
Montenegro (Former Yugoslavia)	10–20	1	
	3,215–4,280	20 or 21 +	

'colonies' spread over a substantial area). The All-Union count of 1986 gave about 1,700 breeding pairs. According to IWRB (Crivelli *et al.* 1994) the former USSR now contains 80–4% of world population, of which Kazakhstan (see Figures 6.1, 6.2) holds about half. In Ili river delta in 1987–89 four colonies in enormous reed-beds held 810–920 nests which is 45–60% of all nesting pairs in former USSR. In addition, this delta supported some 2,500 pairs of great white pelicans. Thus largest population of these two pelicans in Eurasia is in Ili delta, one of last remaining sites of mass pelican breeding (Zhatkanbaev 1994b). At present, areas suitable for breeding pelicans in Ili amount to not less than 740–750 km² or 9% of total delta territory, 44% of water surface. But over last few years permanent colony sites have occupied only 0.095 to 0.1 km²—a minute fraction of area available.

Northern Caspian Sea important; deteriorating rapidly (Rusanov 1997). Breeds in Ural delta and Volga delta, 1974–90 1–5 colonies (25–242 nests).

Greece holds 6–8% world population, at Mikri Prespa (458 breeding pairs, 1995, Pyrovetsi and Economidis 1998) and Amvrakikos; Turkey's Menderes delta perhaps <50 pairs. Up to 35 pairs breed in Gediz delta, W Turkey (Eken 1997). Breeds, again small numbers, in Danube delta from which driven by persecution. Breeds Albania (Camalti Tuzlasi, new colony; Karavosta, old) (Peja *et al.* 1996).

Little more than a century ago this pelican numbered 'millions' across its range from Europe to China. In Central Asia breeds in Chian (Xing Jiang) on lakes of Lopnuv and Postyn and on rivers Haidyg-Gol and Kaidu, and around Karashar, Durbuldzhin and Tarbagatai (Zhatkanbaev and Gavrilov 1994 and references). Lop lake now dry. Figure 6.6 gives remaining breeding grounds and estimates of numbers but other areas not adequately counted.

Useful to count this pelican on wintering grounds worldwide, but not all well-known. Counts best made at night roosts. Crivelli *et al.* (1991b) suggest *c.* 5,500–6,500 birds. Huge decline of Dalmatian due to man, particularly loss of habitat and pollution (see Chapter 4). Where populations small, as in Greece and Bulgaria, subsidiary dangers such

as collision with power lines become important. 93% of casualties immature and this factor alone would cause estimated 1.3–3.5% decrease in breeding birds by time sexual maturity reached. Dalmatian handicapped by strong adherence to traditional sites.

MOVEMENTS: Dispersive and long-distance migratory (recovered over 1,000 km SW of Ili delta where ringed). Deserts colonies end of Jul–Sep though in some areas remains into Nov. Late birds depart once frost begins. Arrives back late Jan–April depending on region. Some migrating populations follow traditional routes with 'stop-overs', often concentrating at favoured locations. For example, birds from northern Caspian Sea fly through Terek delta in Nov and concentrate at mouth of Samur river (Kazakov *et al.* 1994). In mild years some may overwinter here. Large lakes attractive stop-overs. In Sep 1984 more than 1,800 pelicans counted on Aidarkul lake (Uzbekistan). Some Dalmatian and great white pelicans present on Uzbekistan wetlands all year though varying with season; max during autumn migration, which occurs over wide front.

Only important wintering sites in Europe in Albania, Greece and Turkey; some in Iran and Iraq. Major sites: foremost Lake Kerkini (Greece, Pyrovetsi 1990), Amvrakikos gulf (Greece), Menderes delta (Turkey), Caspian Sea shores (Iran), Euphrates–Tigris delta (Iraq), Nalsarovar reservoir (India), Mai Po (Hong Kong), coastal lagoons in Albania, Turkmenia (USSR).

Menderes delta, Lake Bafa and Camalti Tuzlasi, which together hold two-thirds of Dalmatian pelicans in Turkey, used not only by Turkish breeders but also by pelicans from Greece, Bulgaria, and Rumania. However, number wintering in Turkey declined during 1970s and 1980s due mainly to decline in breeding population of Turkey itself. Wintering sites extend from SE Europe to Chinese coast and Hong Kong and differ for different geographic populations. Some Kazakhstan birds visit India. Some immature and non-breeding birds nomadic; in coastal areas of Caspian sea between 2,600 and 5,100 birds wander widely, especially around NE shores and unvegetated spits and islands and shallows rich in fish (Krivonosov *et al.* 1994).

Consequently northern Caspian Sea holds largest group of Dalmatian pelicans occurring within limits of former USSR and future of entire species depends to no small extent on what happens to this group. Nomadic movements of immatures and failed breeders can produce concentrations in non-breeding areas and subsequently formation of new breeding colonies (e.g. Azarov 1994, Shernazarov 1994). In Uzbekistan non-breeding Dalmatians and great whites occur on wetlands side by side with breeding birds during summer months. In Turkmenia in summer nomadic groups fly from lake to lake, staying week or two and then moving on. Alternatively, some immature birds remain on wintering grounds throughout spring and summer. World wintering population estimated, perhaps conservatively, at *c.* 5,500–6,500 birds (Crivelli *et al.* 1991b).

Foraging and food

Adults tend to forage nearer to colony (10–50 km) than great white, though capable of foraging at more than 100 km. Often feeds alone or in twos and threes but described as forming semi-circle and driving fish into shallows. Also noted feeding *en masse* with other species such as thousands of cormorants in Terek Delta and Volga–Caspian channel. However, this communal fishing may be mainly, or solely in autumn, when massive movements of fry of roach, golden ide, and perch occur. On Ili delta in autumn large gatherings of adults, young, and great white pelicans congregate on dried-out lakes, rice-fields and irrigation canals, where opportunistic feeding extends to semi-scavenging of partly asphyxiated or dead fish. Non-breeders (summer) ‘ate a dead horse’, driving herring gulls away (Azarov 1994). Will steal from cormorants, even striking bird as it surfaces (Romashova 1994).

Takes mainly fish, commonly 15–30 cm and 300–1,500 g but range extends from fry up to 50 cm and 2,500 g. Adult’s daily intake *c.* 1,120 g; Romashova (1994) gives 1,500–2,000 g. Av weight stomach contents 1,269 g *n* = 12 and mean weight regurgitates at Mikri Prespa 1984–86: 333, 328 and 262 g respectively. Diet depends on relative abundance of prey species and their availability (seasonal

location, depth, spawning). At Mikri Prespa ate mainly endemic *Chalcaburnus belvica* (Pyrovetsi and Economidis 1998), mean weight regurgitates 384 g. Carp main item in some areas but roach, bream, zander, perch, pike, tench and golden ide locally important. Fry, and sticklebacks (up to 1000 in regurgitates), very significant when feeding chicks. Andrusenko (1994) says sticklebacks caught mainly by unfledged young birds. Could provide important bridge to independence if little (or no) post-fledging feeding by parents. In Albania and Turkey, eels *Anguilla anguilla*, mullet *Mugil* sp and gobies *Gobius buxichichi* main prey, followed by garfish *Belone belone*. Many of these commercial species and this leads to persecution of pelicans by fishermen. In Volga delta main prey is *Cyprinus carpio*, *Abramis brama*, *Perca fluviatilis*, *Rutilus rutilus*, *Blicca bjoerkna*, *Neogobius* sp, *Cobitis caspia* (Romashova 1994). Rarely any evidence of food shortage. In 1992 and 1993 Dalmatian pelicans ate 13.7–16.5% and 19.4–23.3% of mean fishery catch at Karavasta (Albania) (Peja *et al.* 1996) though basis for calculation debatable.

Habitat and breeding biology

(See Fig. at end of ch. 5; Crivelli 1987; Crivelli *et al.* 1991a, 1991b, 1998; Hatzilacou 1992; Poslavski and Chernov 1994; Romashova 1994.)

HABITAT: Often uses more cultivated habitat than European populations of great white; hilly terrain, inland riverine and lakes, often small with islets of floating vegetation. In Omsk region, southern Trans-Ural some breed on lakes in forest-steppe. Practically all breed on vegetated inland freshwater wetlands but *c.* 4% use coastal lagoons around Mediterranean, Adriatic and Ionian Seas due to abandonment of degraded inland wetland colonies. Although typically among reeds and other aquatic vegetation, will nest on open ground. On lagoons, destroys vegetation leading to erosion and disappearance of islets. Apparently does not nest where activities would lead to formation of deep mud, which would incommode such heavy birds and endanger young. May trample areas between nests into hard-packed earthen floor. Despite extensive

loss of habitat, some new colonies have been created. In Turkmenia, some reservoirs with large fish stocks have had suitable nesting islands created but pelicans have not settled.

Breeds gregariously, sometimes mixed with great white or cormorants. Breeders, together with failed breeders and sexually immature birds, use not only area occupied by nests but also adjoining islets and broken-down reed-beds.

COLONIES: In past, large, dense, and traditional. Has marked ability to colonize new sites if previously used ones become unsuitable; otherwise, colonies do not relocate. Everywhere, subdivision of colony into units is highly characteristic. On Mikri Prespa (Greece) size of units (mixed Dalmatian and great white) av \approx 12 nests (range 1–54) (Hatzilacou 1992). Crivelli *et al.* (1991b) give 10.6 ± 8.8 and 8.8 ± 6.1 at Mikri Prespa and Tsoukalis lagoon (Amvrakikos) respectively. Other authors give: 3–6 nests with 2–3 m between groups; 3–20 with 20–70 m; 15–110; 1–22; 3–20 with groups 3–5 m apart or often up to 10–30 m and not infrequently up to 50–70 m apart. Nests within a unit often share common base. Units differ in density of nests (centre-to-centre 60–120 cm) but mean distance varies from year to year. Members tolerant of each other but not of intruders. Close synchronization within units so long as no more than \approx 12 nests (Poslavski and Chernov 1994). However, spread of laying within units varies from 3–29 days and in 1985 no correlation between laying synchrony and size of unit (Crivelli 1987).

Only occasionally are nests situated outside a group and even then they are within 5–10 m of one. Apparently may be competition for site within a group, sometimes resulting in loss of eggs, so that by time young hatch fewer pairs in group than when egg-laying started. Although faithful to a breeding colony (unless disturbed) these pelicans change breeding units from year to year—characteristic of large majority of pelecaniforms. Non-breeders may frequent areas adjoining breeding colonies (Zhatkanbayev 1994) though immature-plumaged birds rare (said to occur ‘in’ colony) and may be driven away by breeders.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Late breeding has led to claims that individual Dalmatian and great white can breed twice in a year, but no evidence; ‘extremely exhausted’ after breeding (Romashova 1994) though quickly regain condition and even lay down fat. Returns to Greece Jan–Feb but several weeks later in north. Pelicans returned to N Kazakhstan 20 March–11 April (1981–90) when steppes and lakes still frozen and sometimes have to feed in ice-free channels; in Ili delta even after incubation begun.

In Greece \approx 9 days between pelicans occupying colony for first time and start of laying. On Mikri Prespa mean date of first egg (1984–89) 7 Mar (range 19 Feb–18 Mar) and at Amvrakikos, 2 Mar (range 5 Feb–19 Mar) (Crivelli *et al.* 1998) a month earlier than sympatric great white. Early breeders may desert in cold spell. Hatching at Mikri Prespa coincided with schooling and spawning of *Chalcaburnus belvica* which continued until Aug, providing continuous food supply (Pyrovetsi and Economidis 1998). On Mediterranean lagoons of Albania and Turkey first eggs laid 15 Feb–15 March irrespective of weather. North of Caucasus lays end March–beginning April, earliest clutches Terek delta 7 April. In Balkans and southern USSR first eggs early April after March return and main egg-laying mid-April–early June. In Omsk region of southern Trans-Ural laying starts early May when ice disappearing, but in some years almost mid-June before laying begins. Preliminaries highly condensed and laying synchronized; spread within a group only 1–5 days. However, in whole colony laying lasts 6–7 weeks or more. Unusually late breeding in Ili delta in 1989 when 80–100 pairs began early Aug, ‘downies’ present Sep (as, also, great white pelicans). In late Oct young still present (Zhatkanbaev 1994a). In general last young independent late July–early August (Greece) and late Sep–Oct in parts of USSR. Non-breeders and failed breeders begin to desert colonies July–Aug.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: (GFA) In N Caspian arrive end Feb or beginning March, in large groups. In some areas vanguard flock arrives 7–12 days before main body.

Birds arrive around midday on calm sunny days (N Kazakhstan) in groups, or occasionally pairs or singles, spiralling in flapping or soaring flight. If still snow and ice pelicans sit quietly but with first sharp rise in temperature behaviour suddenly changes, including frequent aggressive interactions. Behave excitedly and quarrelsomely, sporadically breaking up into pairs. No mention of 'advertising' flights but may be artefact of small colonies now typical of this species.

Aggression shown by threat (open bill with thrust), 'pointing' or, more rarely, overt attack (an exchange of pecks to bill and head, between two or several birds, rather than serious and prolonged fight). Most breeders' bills become scarred through grappling. Stimulus may be attempt by neighbour to steal nest material. No ritualized display with specific function of communicating site-ownership. Late in season recrudescence of male territorial (and sexual) behaviour, with fighting. Attempt to copulate with large young.

Male sexually motivated behaviour includes 'bow' with drooping and vibrating wings and spread tail, bill-snapping and inflation of gular pouch with rhythmic hissing and 'spitting'. Both sexes raise bill, often with extended pouch. Male moves away then rushes back, 'shaking his neck and breast against female' and apparently biting her. On meeting at site partners 'bill-raise' simultaneously.

COPULATION: (GFA)

NEST: Female attends assiduously whilst male brings nest-material 25–40 times per day, reputedly carrying it in pouch. Males gather nest-material communally and quarrelsomely. When delivering material may have to walk over backs of neighbours who apparently rarely react. Female constructs nest in 3–5 days and lays first egg a day or two after completion. Nest large mound grass, reeds, detritus, twigs. Cup lined with fine grass, algae, reed panicles, or leaves. Nest 0.5–1.5 m diameter and a metre or more above water if in aquatic vegetation which is higher than great white and consequently less readily flooded. Eventually becomes consolidated with excreta and flattened. In some localities re-used

annually and increases in size. May form common base with neighbours and such monolithic structure better able to withstand wave action.

EGG/CLUTCH: $91.8 \pm 0.15 \times 59.3 \pm 0.9$; 95 (78–106) $\times 60$ (53–64) $n = 150$; $91.9 \pm 1.03 \times 59.5 \pm 0.67$ $n = 81$; 93.3 (88.3–96.7) $\times 58.7$ (56.2–60.6) $n = 8$; 94.7 (85–102) $\times 59$ (56–63) $n = 29$; 92.2 (83.4–99.8) $\times 59.9$ (55.8–64.5) $n = 100$. Weight: 143–95 g; 171.1 ± 7.3 $n = 81$; 172 (148–224); 170.8 $n = 29$; 176.5 $n = 8$; 189.4 (152.7–213.6) $n = 30$ (fresh). Clutch 1–3 usually 1 or 2; if 4 probably more than one female. Mean clutch Mikri Prespa (1984–89) 1.83 (1.76–1.94); Amvrakikos 1.80 (1.60–1.92). At Camalti Tuslazi and Menderes delta lagoon colonies mean clutches 1.6 and 2.0. In Omsk region 1980–85 mean clutches 2.0; 2.3; 1.8; 1.7; 2.4; overall mean 2.0 ± 0.1 (Blinov *et al.* 1994). Of 330 Kazakhstan clutches 16% held 1 egg, 80.3% held 2, 3.3% held 3, 0.37% held 4 eggs, giving mean clutch-size of 1.88 (Andrusenko 1994) but probably some clutches incomplete. In Turkmenia clutches of 3 av 6.6% of all clutches; in some colonies up to 15.4% (Poslavski and Chernov 1994). Eggs laid at intervals of 1.0–2.5 days. Clutch-size decreases slightly in late clutches.

REPLACEMENT LAYING: Common. Fresh clutches even in June or (exceptionally) late July. Late replacements show sharp decrease in hatching success.

INCUBATION: Eggs incubated on top of webs, starts with egg 1; by both sexes but mostly female. Off-duty but non-foraging parent remains at or near nest-site. Incubation period 30–2 days; 31–4 (captives); 32–3; 31.4 ± 1.4 (wild). Begins with first egg and chicks usually hatch 24–8 hr apart, longest interval 72 hr. No details on length of stints, but female does most; male morning and evening whilst female foraging (Dementiev and Gladkov 1951).

CHICK/BROOD: Hatchling's eyes open; skin pink to red; white down appears day 3 and chick covered by day 9 (Romashova says day 5). Primaries erupt 18–20 days but at *c.* 30 days only 1.5–2.0 mm clear

of sheath. At 45 days body feathered except for head, neck, and rump. Completely feathered *c.* 60 days and begins to fly at *c.* 70 days. Most feathered young grey-white but a minority ochre-white (Andrusenko 1994). Difficulty in determining brood-size since pelican chicks can swim when quite young—7–8 days (Lukashevich 1994) but this surely refers to chicks disturbed from nest and doomed to die. In any case, leads to coalescence of broods. Little if any sibling competition and more than one chick often raised. In Greece 2-egg clutches gave rise to 1.79 fledged young (1985) and 1.92 (1986) compared with 0.87 fledged young per nest for 1-egg clutches (Crivelli 1987); this author states no siblicide in Dalmatian pelican. Only once in 3 years was sibling aggression seen and this not fatal. Mortality of 2nd chick in broods of 2 not higher than that of 1st chick or of single chick (*contra* great and American white). 2nd chick in brood of 2 may be considerably smaller than sibling, and remain so until fledges. Occasionally 3 nestlings in a brood. On Balshoe Beloe in several years 1983–90, Azarov (1994) recorded broods of 4, though may be an artefact; unlikely that all survived.

CARE OF YOUNG: (GFA) Adults tend to arrive with food, often around midday, singly or in small numbers rather than *en masse*, as in great whites. In early stages may change over twice or more per day. At first, adults regurgitate into nest and young pick up food. Later, feed direct from adult's pouch and older young said not to pick up spilt food. At 4–5 days chicks receive whole, small fish at 60–80 g per feed. Later, in two or three feeds may receive up to a third of body weight. An 8–10 day chick receives 200–250 g per feed; at 28 days, 400–500 g. Adults reported to carry water to young in pouch. At first, adults clean nest cup but when chicks downy it becomes soiled, with rotting fish and dead nestlings. Parasites abound. Adults remain on edge of breeding group, avoiding importunate young, which are fed 2–3 times a day. By 20–25 days young mainly left alone, adults roosting and loafing on shore or water near colony. Adults arriving with food late in day may roost on site.

BEHAVIOUR OF YOUNG: Much calling and jostling when parents return with food. Chicks aged 20–30 days may take to water if disturbed, but have difficulty climbing back into nesting area and violently rejected if in wrong group. Early sibling competition described by Andrusenko (1994) but cannot normally result in siblicide since often 2 young reared. Young 20–30 days old gather in pods in centre of 'colony' and these persist at night. After 30–35 days groups move to water's edge. Later disperse and spend much time on water where, from *c.* 40 days, they try to catch fish, usually alone but sometimes in groups of 2–4 and occasionally with young great white pelicans. Return to colony to loaf during day and roost at night. Large young fed away from nest-site, even on water.

FLEDGING: First fly properly at *c.* 70 days; also given as *c.* 80, 84–91, 11–12 weeks. Said to become independent at 100–105 days or to leave area 20–35 days after fledging. Young of coastal lagoon-breeders follow parents, spending more time on barely emergent islands or shoals and returning less frequently to colony.

POST-FLEDGING: Because well-grown young begin to catch for themselves before they can fly properly and whilst still receiving food from parents, difficult to define post-fledging feeding. Certainly brief, if at all. Some fledglings fly with adults to feeding sites away from near vicinity of breeding colony but are probably by that time self-supporting.

BREEDING SUCCESS: Mikri Prespa (Greece), Hatzilacou (1992); Amvrakikos (Greece), Crivelli *et al.* (1998); Tengiz-Kurgaldzhin, Andrusenko (1994); Sarakamysh (Turkmenia) Poslavski and Chernov (1994); Balshoe Beloe (Siberia), Azarov (1994); Albania and Turkey, Peja *et al.* (1995). Hatched from laid: $65.3 \pm 5.8\%$ (55.8–70.3, Mikri Prespa, 1984–89); $52.3 \pm 15.1\%$ (35.5–67.8, Amvrakikos); 90–7% (Tengiz-Kurgaldzhin) which seems improbably high; 25.6 ± 4.0 – $50.8 \pm 6.2\%$ (Sarakamysh, 1984–89, colony visited 2–15 times a season, which may account for low success). Eggs may roll out of nest, be infertile or be abandoned. Avian predation

in Greece low. Low hatching success mostly responsible for poor breeding success. Fledged from hatched, highly variable but difficult to obtain 'natural' figures: $20 \pm 7.4\%$ to $84.8 \pm 6.0\%$ (Sarakamysh). Crivelli *et al.* (1998) say nestling mortality very low. Fledged from laid: $6.0 \pm 4.4\%$ to $43.1 \pm 6.1\%$ (Sarakamysh, 1984–89). Can be zero if much disturbed or flooded. Fledged per pair (often av. 1 chick per breeding attempt but those pairs which succeed in rearing any chicks at all often produce two; figures usually grossly distorted by disturbance): 0.2–1.44 (Tengiz-Kurgaldzhin); 1.03 (0.76–1.20, Mikri Prespa); 0.86 (0.58–1.16, Amvrakikos); 1.16 (1982), 1.21 (1990, Balshoe Beloe), between 1982 and 1990 success varied from 0.7 to 2.0+ per nesting pair; 0.67 (varying between years from 0–0.85, 3 colonies, lagoons in Albania and Turkey). Low success in latter due to poorer quality of breeding habitat and feeding grounds, colonies exposed to wind and to rises in water level after rain, more disturbed with considerable loss of eggs. Foraging probably less successful in lagoons during May–Sep when temperature highest and fishing least productive. Elsewhere decrease in water level (irrigation and drought) allows mammalian predators into colonies, with disastrous consequences. In some localities breeding colonies repeatedly destroyed by fishermen. In 1970s and 1980s Mikri Prespa, Calmati Tuzlasi lagoon, Danube delta, Menderes delta, Lake Skadar and others persecuted in this way (Crivelli *et al.* 1991b). In addition, colonies abandoned due to intrusion by tourists and photographers whilst scientists not blameless. In Turkmenia detailed records of reasons for loss of eggs and chicks up to c. 40 days showed (1984–89) of 921 eggs laid, none taken by predators in 4 years and only from 3–6% in other 2 years. From 1.5–12.8%, according to year, rolled out of nest; from 0–53.8% lost due to storms; in 2 years only, 0.9 and 4.5% abandoned; 0.8–4.8% of eggs 'addled'; 0–7.8% crushed, up to 55.6% disappeared for unknown reasons (Turkmenia). In Greece main cause of egg-loss, rolling from nest (18–24% of total laid), usually early in incubation. Out of 261 chicks, in only one year were any (2.0%) lost to predators. 2.9–6.7% according to year fell out of nest; 0–6.7%

died in nest; in 2 years 4.1% and 2.6% died in colony and 1.5–36.7% disappeared for unknown reasons. Drastic effect of storms in 2 years was due to flooding of nests on low islands. Egg-loss for 'unknown reasons' probably due to poaching and associated predation (natural predation insignificant). Embryonic mortality high ($20.8 \pm 2.4\%$) possibly due to pesticides thinning eggshells. Above authors remark that this pelican's breeding success has risen significantly in last 6 years, denoting pelicans' adaptation to new water bodies, e.g. Lake Sarakamysh, important for conservation.

FIDELITY TO COLONY, SITE, AND MATE: Faithful to colony unless degraded or heavily disturbed. Because of substantial rafts of nests, basic structure often survives from year to year and thus provides incentive to return. No information about natal philopatry but presumably fairly strong, since many colonies persist for long periods. Lack evidence from marked birds but likely that some individuals do return to precise site and therefore that a few pair-bonds may endure from year to year (Andrusenko 1994), though general tendency in pelicans is to change site/mate. Unpublished data (Hatzilacou) states *no* retention of pair-bond year on year.

AGE OF FIRST BREEDING: Said to be mature at 2 years.

NON-BREEDING YEARS: No information.

LONGEVITY AND MORTALITY: (GFA) Adult survival 90% and on present breeding success, population should increase sharply. Not doing so, probably because artificial mortality high. Captive pelicans may live 50+ years. Adult mortality rate unknown but probably 10–15% per annum, excluding death through shooting (serious threat in some areas). In some localities may be greater due to specific dangers such as overhead power lines near colony. Assuming exchange between breeding colonies, productivity data is best fitted by an adult mortality rate of 17.8% and by following breeding scenario: 3-year-olds 60% breed; 4 years, 80%; by 5 years, 100% (Crivelli 1987).

Australian Pelican *Pelecanus conspicillatus*

PLATE 2

Pelecanus conspicillatus Temminck, 1824, New South Wales.

Other common names: spectacled pelican.

French: pélican à lunettes. German: brillenpelikan.

Spanish: pelicanus australianus (Latin nomenclature used in Spanish texts).

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Mainly white with much black. Back white, rump black; upper wing black, broad white patch extends from leading edge; tail black, may be tipped white. Underparts mostly white, sometimes prominent black line well behind leading edge of wing. Head, neck white; yellowish lower foreneck; grey hind-neck. Crest grey, black or white. Breeders develop long tuft of feathers at nape. Often more conspicuous lanceolate pale yellow feathers on lower neck. During courtship bill pink with bluish tinge, prominent dark blue stripe, blue margins become orange towards tip; nail yellow or orange. Pouch mainly scarlet rimmed dark blue. Eye-ring orange-yellow, iris brown. Legs, feet dark blue-grey. Nuptial colours appear *c.* 3 weeks before pair formation; fade soon after nest-site selected.

ADULT F: Similar.

POST-NUPTIAL: Bill stripe changes from blue to red and can be used to recognize incubating birds. Out of breeding season lacks yellow on neck; bill fades to pale blue with pinkish ridge; pouch to pale pinkish-yellow.

JUVENILE AND IMMATURE: Brown replaces black of adult; white wing coverts shorter and more regular than in adult. Bill, throat, eye-ring pinkish. Legs, feet brownish-grey. Immatures similar to non-breeding adults but with shorter white wing coverts.

Field characters

Only pelican in this region but distinguishable from other white pelicans by much more black-brown on upper surface, in sharply demarcated patches.

Measurements (see Appendix)

Voice

Quiet away from breeding colony. Hoarse or guttural groans and belches 'orrh-orrh-orrh' apparently associated with threat and display (pouch swinging, gaping, thrusting); 'thu-thu-thu' (males only, associated with thrusting); 'ah-ah-ahha' (pointing); 'uh-uh-uh' (greeting at nest-site); soft 'oh-oh-oh'. Non-vocal mandible-rattling or clapping. Males bill-snapping during display. Colonies bedlam when large chicks begging 'krr-a-aw', 'wraow-woa-waorr'.

Range and status (Figure 5.3)

Confined to Australasia including Tasmania though wanders more widely (Papua-New Guinea, Indonesia, New Zealand, Fiji). Widespread in Australian coastal and estuarine waters and terrestrial wetlands mainly of open nature. Can breed on very bare, low, offshore islands as on Adele Island off W Australia (see Marchant and Higgins 1990).

Total population certainly hundreds of thousands—*c.* 200,000 bred Lake Eyre 1990; 448 nests on one island 1991 (Kingsford and Porter 1993). Aerial survey (1981–84) Alligator river region (Northern Territory) revealed peak 55,000 pelicans (Morton *et al.* 1993). Although theoretically protected, still killed by fishermen. Utilizes man-made waters and most man-tolerant of all ground-nesting pelicans.

MOVEMENTS: Dispersive. As inland areas dry, may move in spectacular numbers. Occurs in some coastal areas and may wander to offshore islands. Apparently no regular or predictable pattern to movements.

Foraging and food

Often exploits temporary inland wetlands especially if these are receding and concentrating ephemeral prey. Tolerates wide range of depth, temperature, turbidity, salinity and exposure. As a cooperative feeder it likes pools and channels with dense prey. Fishes in dams, reservoirs, and drainage channels; not afraid to feed in urban parks and marinas though cannot breed there.

Extremely versatile. Often cooperative day-time feeder but will feed singly, or at night. Will plunge superficially from 1–2 m submerging at least head and neck. When feeding cooperatively swims in loose line, wings partly open, driving fish ahead into shallower water to be scooped up. Fish include, importantly, goldfish *Carassius auratus* and perch *Perea fluviatilis* up to 27.4 cm and 320 g. Weight of single regurgitate (7 goldfish) 870 g. Does not disdain crustacea (crayfish *Cherax destructor*, shrimps *Macrobrachius* sp), insects, carrion, small mammals or birds such as ducks and gulls. Feeds opportunistically on land; will rob other species. Carries food in gullet, not pouch.

Habitat and breeding biology

(See Fig. at end of ch. 5; Vestjens 1977; Marchant and Higgins 1990.)

HABITAT: Low-lying islands or secluded coast, or inland on lakes, swamps, rivers, where undisturbed and preferably free from land predators (at Lake George cattle and sheep grazed, dogs disturbed breeders leading to great loss). Presumably will not commence breeding under these conditions but may be overtaken by them. If breeding among vegetation, including bushes, will tread it down to form a base. When exploiting ephemeral inland waters will not nest until these flooded for at least a year; presumably allows development of adequate amount of food. Small breeding groups inconspicuous; at a distance, easily mistaken for loafers.

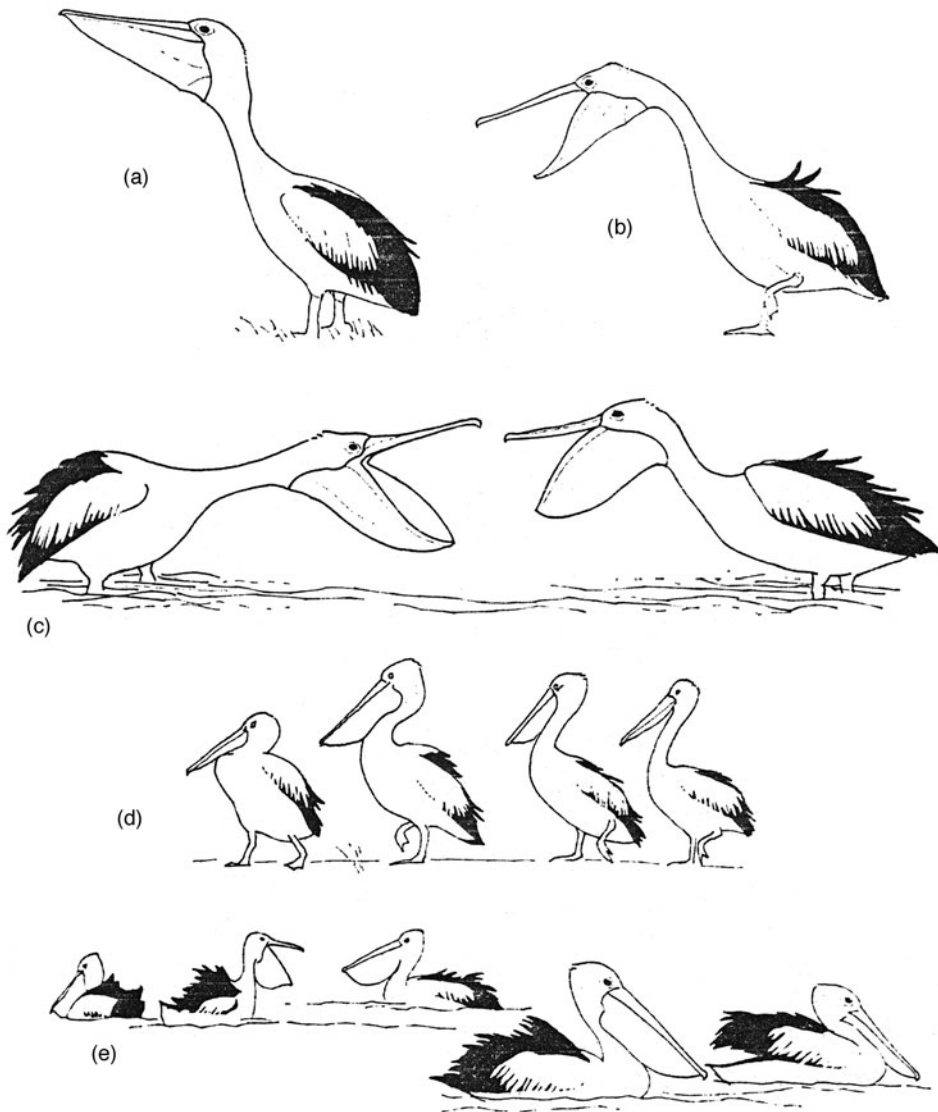
COLONIES: Often large and dense, with nests less than metre apart. Centre–centre distances usually 80–90 cm but some nests touch. Defends only nest-site. If contents lost and nest deserted, other pairs may take over. Location of colony may persist for several years, be abandoned and then recolonized.

FREQUENCY, TIMING AND DURATION OF BREEDING: No evidence that can breed more than once a year. Birds concentrate near future nesting area *c.* 4 weeks before breeding. Reliable data too few to detect strong seasonal trend; eggs found any month. Breeding depends on factors influencing food, drought, rain, and associated water levels. Three widely spaced visits to Adele Island, W Australia, June–July, all revealed fully grown young, indicating wide spread of laying. Needs at least 3 undisturbed months and assured food supply to breed successfully. Breeds opportunistically to utilize floods.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Fights infrequently; may grab and hold opponent's bill or twist its head sideways and with wings busked intersperse pecks on head and neck. Threat between males employs 'pointing', 'gaping' and 'thrusting' (Figure 6.7), with accompanying vocalizations, all as part of complex communal interactions involving both sexes and several—sometimes many—birds. Small groups may coalesce, this larger unit then fluctuating in size as birds mill around and females lead retinues of males in different directions. This 'following' behaviour occurs on land, water, or in the air. If on water birds may then take off, female leading, and circle nesting area. If on land (even flattened tops of lignum bushes will do) males, with open bill, swing their pouches, thrust bills at each other and pick up, throw, and catch various debris. Eventually only one following male remains. As the putative pair approach a potential nest-site both may 'bow', arching neck and pointing bill downwards and/or obliquely upwards. Once there, do not display further but may sit, preen, stretch or even depart after minutes or hours. The combination of lateral and vertical head movements (swinging downward-pointing bill from side to side and up and down) performed when courtship walking or swimming, is accompanied by conspicuous 'pouch-rippling' (both sexes), 'waves' moving from throat to bill-tip. Simultaneously 'clap' bill.

COPULATION: (GFA)

NEST-BUILDING: Apparently female selects nest-site and initiates nest-scape. Scraping behaviour,



6.7 Threat and courtship in the Australian pelican. (From Vestjens 1977.)

closely associated with copulation, occurs sitting or standing, using bill to loosen substrate under or alongside body. Repeatedly scoops material into bill and throws it forward, using upward jerk. Or may anchor bill in substrate and use one foot to push sand backwards, occasionally shifting bill, pivoting slightly and repeating procedure. Male may gather material from distance (1 km+) but brings

back only one piece per trip, held in bill. On return displays to partner (both perform 'head-up'). May drop material in front of female ($n = 247$), allow her to take it from his bill ($n = 151$) or add it directly to nest ($n = 22$). Female gathers surrounding debris using sideways shovelling movement or picking up items. Material added during incubation and whilst small young in nest. Nest variable

mound of assorted flotsam if on ground; scrape $n = 28$, 54 mm (45–70) deep, 315 mm (210–370) diameter, surrounding material and lining added later. If in lignum bush, trampling provides base and structure varies greatly according to availability of material. May be up to 3 m above ground or water; diameter 625 cm (510–720) $n = 21$. One nest contained $c. 200$ items 12–220 cm long.

EGG/CLUTCH: 90 (83–96) \times 59 (54–63) $n = 60$; 90 (81–96) \times 57 (54–64) $n = 32$; 93 (85–98) \times 57 (53–9) $n = 15$, positions within clutch not known. Weight: 168 (148–208) $n = 17$ (not certain fresh). Each egg $c. 3.4\%$ female weight (figure for latter approx, correct % probably lower). Clutch most commonly 2; larger clutches (up to 4 recorded) probably involve rolled-in eggs. Clutch $c. 7\%$ female weight. First egg laid 2–3 days after settlement at nest-site, 2nd within 4 days of 1st.

REPLACEMENT LAYING: Not clearly demonstrated but probable under right conditions.

INCUBATION: Shared about equally, males usually in morning and females afternoon. Eggs incubated on top of webs. Displaced eggs rarely retrieved. During nest-relief partners perform mutual 'head-up' display after arriving bird has 'bowed'. Incubation period 32–35 days. Stints usually 2–10 hr, occasionally longer.

CHICK/BROOD: Hatchling pinkish, eyes open, short grey down within a week. Colour of iris, bill, orbital skin, down on head and neck variable, but differences between individuals disappear during growth. By week 8 well feathered in parts including black dorsal feathers. Remain in crèche until $c. 50$ days; may then take to water.

Apparently does not rear two chicks. Contribution of second egg not documented and no details concerning brood-reduction.

CARE OF YOUNG: (GFA) At 1 week (Vestjens says 2) briefly move out from beneath adult. Small chicks sip semi-digested food from trough of vertically held upper mandible (Figure 5.9). Later may even stand in parent's pouch. After 25 days left

during day, after $c. 30$ days may form pods of up to 30. Young fed in nest or from crèche. Feeding rate drops from up to 8 times per day to 2 per day at 30 days, once per day by 80 days.

BEHAVIOUR OF YOUNG: Vestjens suggests chicks crèche outside colony because continually harassed by adults due to lack of space. However, crèches important in thermo-regulation. A newcomer crawls onto backs of outermost chicks and drops down into a space. Crèches move, fluctuate in size, and remain in breeding area until young can fly. Small young return to nest to be fed; food regurgitated as result of disturbance may be re-eaten. Larger young fed in or near crèche. Very large young may travel many metres to meet parent; may receive food on water. Chicks often convulse after feeding (GFA). In nest or crèche may fight, large young attacking smaller, by pecking head and neck. This may provoke more general attack resulting in expulsion from crèche and, in 2 observed cases, death. Comfort behaviour largely as adult once chicks $c. 50$ days but, unlike adults, will allo-preen.

FLEDGING: No details. Flies $c. 80$ days; usually moves from immediate vicinity.

POST-FLEDGING: Not known to be fed once fully free-flying, though some return to be fed weeks after taking to water.

BREEDING SUCCESS: (Vestjens 1977) Hatched from laid: 66% ($n = 130$, but not clear that hatchlings related exclusively to these eggs). Fledged from hatched: 44% ($n = 86$, 49 reached crèche stage, cannot be taken as representative since much variation between localities and years). Fledged from laid: 22% ($n = 130$, too low to maintain stable population, so presumably atypical). Total failure not uncommon. At Lake Cowal, in only 3 out of 6 seasons did any young fledge. Main loss may be due to parading and displaying members of colony whilst others laying or incubating. Hence, synchrony of individual groups presumably highly adaptive. Young may be lost due to disturbance by dogs or cattle. Fall of water level exposes them to predation or disturbance, causing

270 American White Pelican *Pelecanus erythrorhynchos*

huge losses (hazard of opportunistic breeding). No evidence that starvation common.

FIDELITY TO COLONY, SITE, AND MATE: As partly opportunistic breeder, not tied to traditional colonies, though some probably occur. Mates and sites not retained for successive breedings and partners not known to associate far from nest-site.

AGE OF FIRST BREEDING: Matures 3 or 4, but range at which first breeds unknown.

NON-BREEDING YEARS: Vestjens remarks on bill and pouch colour of what he calls non-breeding birds, which he distinguishes from immatures. No details otherwise.

LONGEVITY AND MORTALITY: Not known; can live 60 years in captivity (Grummt 1984). Life-history data inadequate to calculate reliable mortality rates.

American White Pelican *Pelecanus erythrorhynchos*

PLATE 2

Pelecanus erythrorhynchos Gmelin, 1789, Hudson Bay and New York.

Other common names: rough-billed pelican.

French: pélican d'Amérique. German: nashornpelikan. Spanish: pelicano Norteamericano, pelecano blanco, alcatraz blanco,

ADULT F: Similar.

POST-NUPTIAL: Bill, pouch, facial skin become pale yellow-green; horn disappears; eye skin blue-grey; legs, feet pale yellowish; head feathers short; neck feathers downy; plumes lost on nape, lost or much reduced on breast, wings.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Largely white with conspicuous black primaries, primary coverts, some secondaries. Lesser upper wing-coverts pale yellow, lanceolate plumes; stiffened lanceolate feathers, also pale yellow, on upper breast. Head, neck mainly white; long, narrow plumes on hind neck and nape form short, erectile, pale yellow crest. Hind neck sometimes dark coloured with mottled ear-coverts. Legs, feet orange. Eyelids scarlet, iris brown. Facial skin yellow, more orange around eye. Pouch mainly orange with distal third whitish, sometimes mottled black, orange-yellow at base. Bill orange or pink, whitish ridge on upper mandible. Conspicuous fibrous horn about one-third from bill-tip, upper mandible. Horn \approx 51 mm long (17–85), 41 mm high (26–57) weighing 10 g (2.9–24.3). Acquired early in breeding season, usually shed after eggs laid.

JUVENILE AND IMMATURE: Brownish with dark crown. Bill, pouch pale grey. By first spring largely white except for black wing feathers but no breeding adornments. Final adult plumage possibly not attained until 3rd or 4th year.

Field characters

Only white pelican in region. Otherwise adult at distance could be confused with great white. Juvenile American much whiter than juvenile great white.

Measurements (see Appendix)

Voice

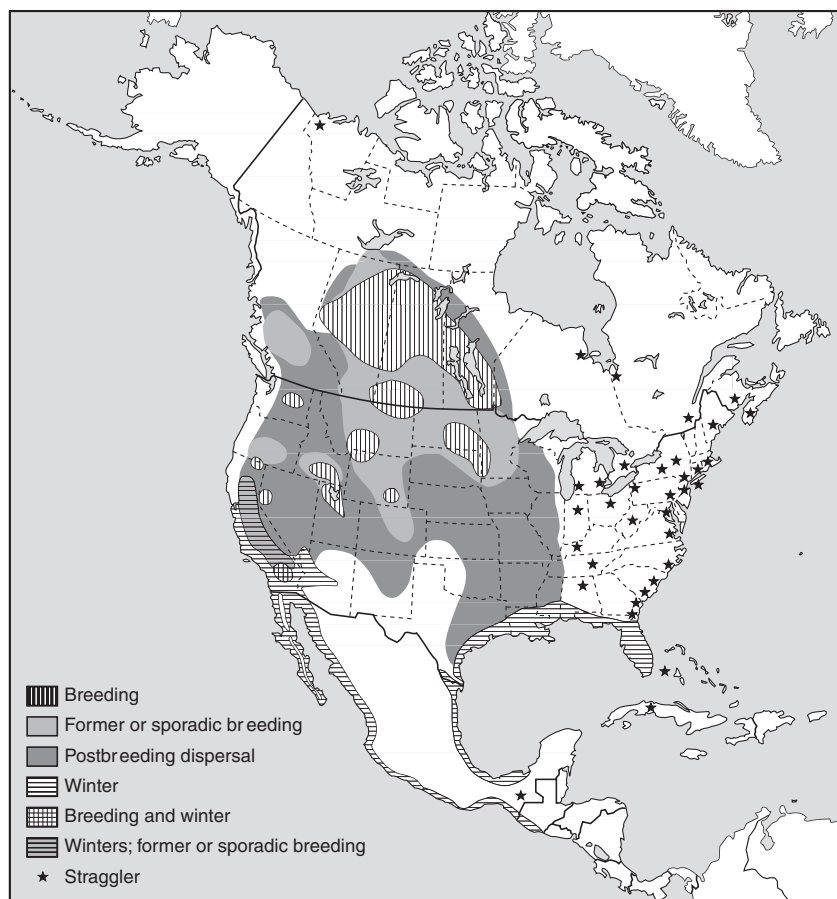
Harsh, nasal growls and grunts during aggressive interactions at colony; loud, nasal 'ho-ho-ho' during display at nest-relief. Loud, harsh grunts during copulation. Croaks. Small young beg with harsh 'kek-kek-kek' and later with nasal 'waa-o-waa-o'. Non-vocal sounds are rapid bill-clapping (Evans and Knopf 1993 say no bill-clapping display) and single snap of bill directed against own and other species.

Range and status (Figure 6.8)

After dramatic decline since early 1900s has recently stabilized and may have increased in parts of USA and Canada in 1980s. Confined as widely scattered colonial breeder to W of N American continent from Canada to California, W of Great Lakes in Canada and N of 40° at in western N America. Local in British Columbia and N and E Alberta, central and S Saskatchewan, S W Manitoba and S W Ontario. In recent years in USA has bred in California, Oregon, Nevada, Utah, Idaho, Wyoming, Colorado, Montana, N and S Dakota, and coast of Texas. Also, at least sporadically, in Laguna Madre de Tamaulipas and Laguna

Santiaguillo, Durango (Mexico). Colonies may be traditional or spring up in places previously unoccupied (details Evans and Knopf 1993; Johnsgard 1993).

Smith *et al.* (1984) said 16,000 birds W of Rocky Mountains represent 16% of continental population; implies *c.* 100,000 birds for total continental population. In 1967–69 *c.* 30,000 birds believed to breed in Canada; 1970 *c.* 1,000 in Mexico, 1971–72 *c.* 33,700 in USA, indicating world breeding population 1960s–70s of *c.* 65,000 birds (Clapp *et al.* 1982); to this must be added pre- and non-breeders. From 1972–82 on 'Blue List' of American birds of special concern later downgraded to 'local concern'. Crivelli and Schreiber (1984) give results of accurate and complete survey (1979–80)



6.8 The distribution of the American white pelican. (From Palmer 1962.)

as 52,000 ($\pm 5\%$) nests in 14–17 colonies in USA, 33,000 nests in 50 colonies in Canada (mainly Manitoba with 14,700 nests in 32 colonies; cf. Koonz and Rakowski (1985) who give 14,000 nests on 36 islands, and Saskatchewan with 15,400 nests in 19 colonies). Crivelli and Schreiber conclude earlier estimates too low. Using their figures, world population would be USA 104,000 ($\pm 5\%$), Canada 66,000, plus Mexico $\approx 1,000 = 171,000$ breeding birds, to which must be added pre- and non-breeders. Numbers had declined dramatically since early 1900s but population increased $\approx 5.3\%$ per year from 1966–91 (Evans and Knopf 1993). Previous decline in population and contraction of range not merely episodic. For example, used to be at least 24 colonies in population W of Rockies whereas now only 8. And despite S Texas remaining relatively constant at 200–500 nests, this century population has fluctuated from apparently none to 2,500 (Chapman 1988).

MOVEMENTS: Largely migratory and dispersive, moving overland in flocks, far from breeding haunts. Although some areas, such as S Texas, may have birds all year, may be different individuals. Winters inland and along Pacific coast from north-central California and central Arizona S to Mexico and Guatemala and from Florida along Gulf of Mexico to Tabasco (see Figure 6.8). Spring migration, Feb–May; breeders arrive most colonies mainly April–May. Non-breeders and pre-breeders (i.e. birds too young to breed, say 2 years old) continue to arrive later. Autumn migration Sept–early Dec preceded by movement to ‘assembly’ areas where thousands may gather, though they do not depart *en masse*. Juveniles may move in stages. Pelicans from different regions appear to have own loose wintering areas though birds from several regions may use same area if they coalesce on migration. However, populations breeding E of Rockies migrate mainly SE whilst those W of Rockies move S and W and rarely E to Gulf coast (Evans and Knopf 1993). Individuals wander widely and turn up in unexpected places.

Foraging and food

Feed in shallow water in marshes, lakes, and rivers. May forage hundreds of km from colony though

mostly in wetlands within 75 km (Findholt and Anderson 1995b). Travel in flocks and use thermals. O'Malley and Evans (1982a, 1982b) indicate that foraging flocks do not form as result of random departures from colony followed by chance coalescence *en route*. Rather, departures clumped in time suggesting tendency for one bird to follow another. Often, birds flew short distance in direction of foraging area before alighting on water. When others approached or passed, they followed. Or circled nesting area and joined by others before setting off. Flock-size highly variable (up to 253) and showed no seasonal trend. Large flocks flew in V and J formation, small ones in simple lines. Angles in formation (24–122) greater when birds closely spaced. Frequency of wing-beats and proportion of time spent flapping lowest in V formations and greatest in single birds. Leading bird usually flapped most. Seems that formation-flight more economical than single flight. Presumably, also, communal feeding adaptive. O'Malley and Evans (1984) showed that birds arriving at foraging-site selectively joined larger-than-average foraging groups and suggest this facilitates food-finding (for further discussion of coloniality and foraging see Chapter 3). Aerial surveys of pelican activity in S Oregon and NE California showed that 66% of all pelicans observed on ‘ground’ were foraging; others loafing (Smith *et al.* 1984). Between 08.00 and 11.00 hr 78% foraging. Foraging concentrated along shorelines but also inland in canals, ditches, and ponds.

Although described as cooperative feeder, encircling fish and driving them into shallow water, also forages singly or in small, uncoordinated groups. McMahon and Evans (1992a) separated several foraging strategies based on presence or absence of grouping and on differences in locomotion, flock-shape, and degree of coordination of movements and synchronization of bill-dipping among members. At most coordinated, bill-dipping almost perfectly synchronized, usually in half-circle but occasionally closed one. Uncoordinated aggregations rare. Significant differences in success of different strategies. Capture rates within two most highly coordinated usually better than for others (cf. great white pelican). Anderson (1991) noted that members of groups of 2–6 caught significantly more

than either singles or larger groups. Strike-frequency reached upper asymptote at flock-size of 4.

Nocturnal foraging important; 2 or 3 times as many foraged at night as during day, in larger flocks (McMahon and Evans 1992b). Capture rates highest for daytime flocks of up to 100 but this relationship did not occur at night. Night-time dipping rates higher but capture rates lower, though fish caught tended to be larger.

Diet almost entirely rough fish (e.g. large mouth bass *Micropterus salmoides* and bluegill *Lepomis macrochirus*), crustacea and (extensively) amphibia. Over 2 seasons, salamanders comprised 49.7–64.4% of total food (Lingle and Sloan 1980). In Wyoming, May–Aug, 84% by mass of food were suckers (*Catostomus* spp) but took more trout after stocking (Derby and Lovvorn 1997b). Also Wyoming, 584 regurgitations gave 24 prey species, more than 90%, numerically, Iowa darter (*Etheostoma exile*), salamander (*Ambystoma tigrinum*), minnow (*Pimephales promelas*), sucker (*Cotostomus commersoni*); 83% biomass common carp (*Cyprinus carpio*), suckers, salamanders (Findholt and Anderson 1995b). Smith *et al.* (1984) noted feeding on spawning carp in flooded fields. Birds from S Oregon to N E California fed mainly at lake not only further from nesting colony than other feeding areas but with fewer fish (shown by gill-net samples). Adult consumption $\approx 1,800$ g per day; 67.5 kg needed to rear one chick. On coastal lagoons, Mexico, pelicans estimated to eat 4.1 kg per hectare per day (Acuna *et al.* 1994).

Kleptoparasitism not uncommon. In one month O'Malley and Evans (1983) noted 36 instances of pelicans stealing from other species, mostly gulls—also double-crested cormorants (Anderson 1991) and great blue herons—and 32 attempts to steal from other pelicans, of which 12 successful. Attempts to steal merged into joining successful birds in coordinated search.

Habitat and breeding biology

(See Fig. at end of ch. 5)

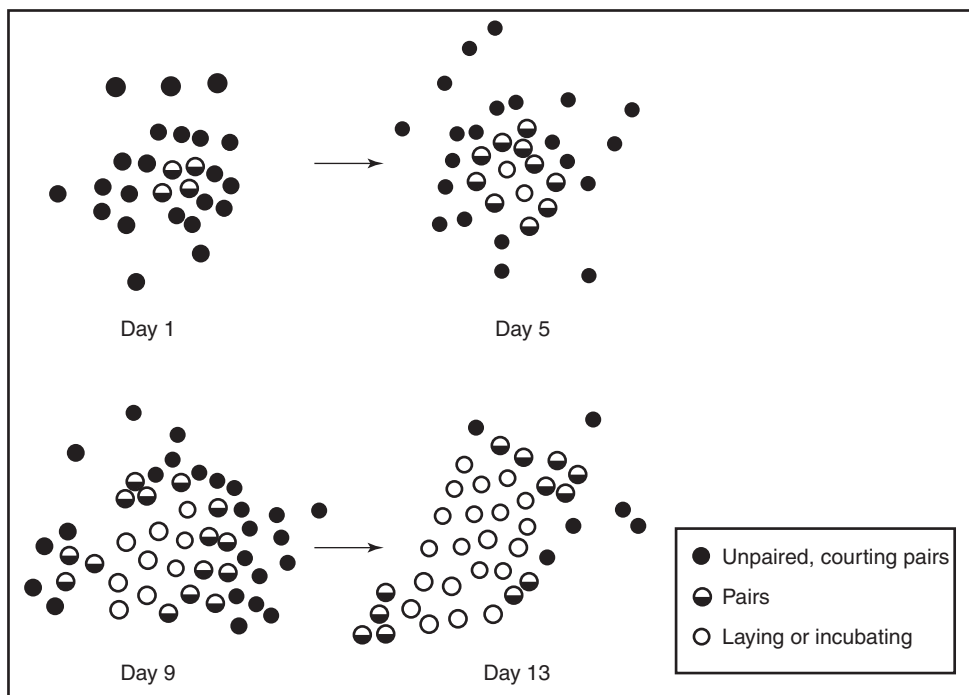
HABITAT: Predominantly freshwater though wintering birds will feed in marine bays and estuaries. Breeders vulnerable to disturbance and require inaccessible locations even if distant from food sources.

Nest on flattish, isolated, bare islands in freshwater lakes. In Manitoba tend to colonize clusters of islands in large lakes, with main colony and several satellites; typical where populations increasing (Koonz and Rakonski 1985). Some colonies repeatedly abandoned, even late in incubation; cause unclear, disturbance possible. May be deserted if water recedes and mammals enter. At Gunnison Island nests on loose soil, sand, grass, or among driftwood or shrubs (Knopf 1979). Colony on Klamath Lake, Oregon, on floating tule islands. May nest with double-crested cormorant.

COLONIES: Most fairly small; sometimes large—Chase Lake, N Dakota, holds 8,000–10,000 birds though not in single mass and in Manitoba some islands hold more than 2,000 nests. Johnsgard (1993) gives distribution colony sizes (birds, not pairs): 1–50 (6), 51–100 (3), 101–200 (5), 201–500 (11), 501–1,000 (5), 1,001–2,000 (9), 2,001–5,000 (12), 5,001–10,000 (5), over 10,000 (1).

Colonies of hundreds rather than tens of pairs contain discrete clusters separated by gaps or by differential timing of breeding. On Gunnison Island groups ranged from 2–633 nests, often fewer than 50 but frequently up to 175; mean distance to nearest neighbour nests $0.59 \text{ m} \pm 0.16$. Nests at Yellowstone much denser (centre to centre 0.11 (0.07 – 0.19)). But both colonies had much unused space indicating that clustering is a social phenomenon. Elsewhere, centre to centre $1.06 \pm 0.2 \text{ m}$ $n = 172$.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually. Some populations strongly seasonal. Early birds, often at colony whilst ice on nearby waters, may arrive up to 3 weeks before pairing. Pelicans arrive Yellowstone Park av 11 May; laying usually begins ≈ 25 May but variable. In Oregon and California hatching mainly late May–early June thus laid early-to-mid-May. Great Lake colonies mid-April–early June; N Dakota, mainly June. On Gunnison Island, Utah, late March–early May (75% nests initiated 9 April–6 May); up to 6 groups established each week, often widely separated. Synchrony such that in 16 groups first egg hatched in 90% of nests within 2–9 days of each other, independently of group size. Thus



6.9 Colony formation in the American white pelican. (After Knopf 1979.)

group synchrony marked, though colony as whole may contain hatchlings through to fully grown young. Since, later, pod-formation has highly unsettling effect on pairs still incubating or brooding, sometimes causing desertion, such synchrony adaptive. Because colony divided into many groups, high proportion are edge as against centre nests, suggesting little advantage to latter (*contra* apparent situation in some seabirds). Percentage of nests abandoned rose steeply in relation to lateness of their first egg (Knopf 1979). Similarly, mean number of chicks fledged per nesting attempt dropped from *c.* 1 for early nests to 0.1–0.3 for very late nests. Nevertheless some ‘colonies’ only roughly synchronized or divided into poorly defined, asynchronous sub-colonies (e.g. Smith *et al.* 1984).

Before breeding begins, soaring flocks of unmated pelicans over breeding ground attract others to active site, thus facilitating synchronous breeding groups (Knopf 1979; Evans and Cash 1985). Newly arrived birds attracted to area over

which most flights occurring. From such flocks small groups occasionally stooped with loud ‘whooshing’ sounds. Some time after arrival pelicans joined dense aggregations of groups at different stages of breeding, some already with eggs but others still courting. Within these groups, apparently, pair-formation occurs.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Overt fighting occasional but brief. Threat-gaping, sometimes with head waving. Aggressive jabbing and bill snapping from established birds towards intruders. Males return such jabs whereas females ‘bow’ (see below). No specific, ritualized site-ownership display described.

Initial interactions between sexes occur in group near to or among established pairs. Courting groups later become nesting groups (Knopf 1979). Female responds to male ‘jabbing’ by raising breast, lifting wings and arching neck to bring bill-tip to breast (‘bowing’). Male may then move alongside, reaching

over female's head with expanded pouch and grunting, but female may rapidly move on, leaving male behind to repeat process. Male and female may leave display group and parade around, male in 'strutting' walk, head plumes erect. Other males may join in, creating a courting party. Female may take off followed by males (courtship flight or circle-flying), one of whom stays near female, expanding pouch and grunting. After few circuits two land and continue strutting walk whilst surplus males abandon. During strutting (heads up, bill down) male may jab back of female's head and she bows. Approach to incubating or brooding birds elicits jabs; female again bows. Eventually pair may return to area containing unmated and paired birds and at some point begin to retaliate to any jabs and (both sexes) to bow. At this point Knopf (1979) implies that they have defined their site. Grummt (1984) observing captive birds, says male selects site; in wild typically adjacent to others at similar stage in breeding cycle. 'Head swaying' (slow side to side head movements in horizontal figure of eight) occurs during late courtship and nest relief.

COPULATION: (GFA)

NEST: On ground. Pair remain at or near nest-site for 3–5 days after pair-formation, building and changing-over on nest. Central cup unlined, only ≈ 5 cm deep. Sitting bird rakes various materials to form mound round scrape up to 28 cm in height, 56 cm diameter at top and more at base. No mention of digging with bill or scraping with foot but these basic patterns unlikely to be absent. Apparently items not carried to nest in bill; presumably in pouch. Material added so long as young in nest. Nests may be washed out by extreme water levels.

EGG/CLUTCH: $87.01 \pm 4.47 \times 56.14 \pm 2.17$. Extremes 103×54 ; 81.5×62 ; 62.5×45 ; 85.5×34 $n = 62$. Weight ≈ 150 g; 154.2 (134.5 – 187.2) $n = 26$ (fresh). Weight of fresh egg (1st in clutch) 2.0–3.4% female weight. Yolk 17.5% egg contents. Shell thickness has recovered after thinning in late 1960s (Bugden and Evans 1997).

Clutch usually 2. At Yellowstone 66.5% nests $n = 212$ contained 2 eggs; 32.5% 1 egg, 1% 3 or 4, counts after most birds incubating >2 weeks. In Texas, mean clutch 1.9 $n = 10$; S Dakota 1.95 $n = 20$. Laying interval 2 or 3 days. Second egg acts as insurance, surviving at $\approx 20\%$ of nests in which first chick fails to survive (Cash and Evans 1986, Evans 1997). Latter found that, hatched in laboratory, egg 2 slightly less efficient at converting egg-size into hatching mass. Selective desertion of second egg not been reported but signs of neglect noted. Two days (mean) elapse between egg 1 and egg 2.

REPLACEMENT LAYING: Suspected; instances may have related to different birds.

INCUBATION: Eggs laid 4–6 days after pair formed and site selected. Guarded or incubated continuously, sexes sharing for 31.5 ± 1.20 days $n = 13$; 28–30 days (captive). Covered by webs, one on each egg, rather than eggs placed on webs; turned ≈ 3 times/ day. At nest-relief 'head-up' and 'bow' (both sexes) repeated without definite sequence and accompanied by nasal 'ho-ho-ho', displacement preening, and handling of nest-material. Relieved bird may walk off with beating wings. Nest-relief ceremony becomes cursory as young grow. During incubation change-over av 1 per 2 days mostly mid-morning to mid-afternoon. Time varies; av 8 min (1 min to 1 hr or more). Relieved bird remains by nest for av 4 min. Once more advanced young begin to form pods, breeding of later pairs is disrupted because inclined to join loafers, thereby losing their eggs or small young—a danger which increases advantage of breeding synchrony.

Incubation and hatching studied in detail (Evans 1988a, 1988b, 1989, 1990a, 1990b, 1992). Chick calls trigger removal of webs from on top of egg to beneath, as in gannets. At onset of pipping, eggs incubated between adult's legs; chick takes ≈ 1 day after pipping. Eggs hatch $\approx 2.5 \pm 1$ days apart (Evans and Knopf 1993). After chick 1 hatches temperature of egg 2 can temporarily drop to 29°C . When one egg of clutch failed to hatch

($\approx 1\%$ $n = 420$) it contained well-developed embryo (Knopf 1979).

CHICK/BROOD: Hatchling orange skin; eyes open first day; weight 110 g. Vocalizes 'kek-kek'. Growth variable. Culmen growth linear up to at least 30 days. Day 10, body well covered with white down. Cannot control body temperature until day ≈ 16 , though Abraham and Evans (1999) say modest degree of endothermy by day 7.

Visible shivering by day 7 increases thereafter. Gular fluttering from day 1 (Evans and Knopf 1993 for details). By day 17 some young left unattended. By day 22 brooded only intermittently by day but attended overnight. Day 28 usually left unattended at night as well as day. Day 69 almost full-grown. Eggs hatch asynchronously and usually only one chick reared. On Gunnison Island, in nests where both eggs hatched, one chick died in just over 90% of 569 nests in 1973 and 1974 (Knopf 1979). Deaths occurred during week 1 (15 cases), week 2 (38) and week 3 (36). However, in important contrast to great white, American white reared 2 chicks in 44 out of 382 nests, mainly on periphery of group and usually neighbour to a nest which also reared two (Knopf 1979). Birds rearing two had laid eggs before 15 May. Brood reduction not obligative; though marked sibling aggression, main cause of death exclusion from food—a more flexible mechanism than innately programmed siblicide. But direct aggression by older chick nevertheless important. Even if does not kill sibling directly may cause death from exposure or predation. Evans (1996) supports hypothesis that second egg is insurance and showed high probability 'B' chick surviving early period (5–7 days) of death of 'A'.

CARE OF YOUNG: (GFA) Parent regurgitates semi-digested food, pointing bill downward and backward, at first on to ground or webs, then from near tip of lower mandible and by day 10 near top of pouch. Although in early stages may feed chicks up to 4 or even more times per day, later mostly single bout per day, each parent returning to colony every 2 days (Cash and Evans 1987). Adult lands, feeds young (bout lasting min or less) and departs within ≈ 5 min. Still feed young daily at 10 weeks (about to fly). Fish up to 68.6 cm fed to young.

Nearly fledged young regurgitated av 1,200 g $n = 50$. Amount of food per chick per day ≈ 227 g at 10 days, 908 g at 30 days and 1,816 g at 55 days.

Apart from close-brooding when chicks very small, adults not notably attentive; do not alter position to shade young nor brood them during day if they are cold.

BEHAVIOUR OF YOUNG: (Schaller 1964, Evans and Knopf 1993) Hatching and (later) thermally dependent chick controls temperature by increasing squawks when it is cold, which stimulates adult to warm egg or brood chick (Evans 1992, 1994). Neonate has distinctive begging call which, as shown by playback, can elicit adult's feeding posture. Small chick takes food from ground. At day 7 pesters parent's bill, tries to insert head into pouch and calls harshly, 'kek-kek-kek'. Large young beg on belly with beating wings and nasal call; take food directly from gullet of standing parent. Adult may disengage violently. Occasionally 2 young feed simultaneously but most broods soon reduced to single chick. Preens by ≈ 14 days, stretches wings, can vibrate pouch (thermo-regulation?). Can crawl by day 17, walk unsteadily using wing-tips for support by day 20, walk well and take to water if disturbed by day 28. By ≈ 1 month all young have joined pod, where occasionally may be brooded by parent. At this time first occurrence of ritualized displays 'head-up' and 'bow'. By day 33 defends against, for example, gulls, by jabbing; may bathe in adult manner.

Pods, small at first, coalesce until, by about 2 months young form one large pod combining chicks from several groups. In bad weather, huddle at night. Apparently around pod-formation stage, convulsions associated with feeding begin (GFA). Parent and young appear to recognize each other, visually, aurally or both, when former returns with food. Strange young may importune, but unsuccessfully. Adults may attempt to mate with large non-related young, possibly stimulated by resemblance between female soliciting behaviour and posture of begging young.

FLEDGING: Day 69, glide a little downhill; day 72, can fly and swim far. Fledging period 12–13 weeks according to some, 9–10 according to Evans and Knopf (1993) who say they depart

from colony at 10–11 weeks, one week or more after first flights.

POST-FLEDGING: Depends on definition of fledging. Some young fed after they can fly and at distance from colony, but probably not for long if at all.

BREEDING SUCCESS: (Gunnison, Knopf 1979; Evans and Knopf 1993) Hatched from laid: unlikely to be much higher than 60%. 592 eggs from 2,261 nests and 7.7% nests with chicks abandoned, 1973, 1974, Gunnison Island. Nests on edges of groups more prone to desertion than central ones (24.5% against 14.7%). Also, eggs lost steadily during incubation 8.3% of 242 eggs (1973) and 9.9% of 222 eggs (1974), rolled out of nest presumably as result of change-over, egg-shifting and perhaps interactions between neighbours. Nests with only one egg rose from 7% in week 1 to 20% by week 4. Fledged from hatched: one egg from clutches of two almost always fails to produce a fledgling but fledging success of surviving chick is high (85%+); 0.85 chicks per clutch fledged in herbaceous, bare, and shrubby areas, and 0.89 in sites among driftwood. Some entire groups reared no chicks whilst others averaged one per pair. Fledged per pair: 0.54; 0.39. At Sand Lake, S Dakota, 14 nests hatched 28 chicks but only 13 fledged. At Molly Islands (Yellowstone), 20 years, no chicks in 5 years, 302–650 in

further 6; overall mean 214 ± 196 SD (baseline breeding population 546 ± 183 SD, Diem and Pugesek 1994). Independently of group-size; pelicans in small groups showed highest and lowest mean production. Ones settling near already established groups generally failed to produce young, again suggesting adaptive value of group synchrony.

FIDELITY TO COLONY, SITE, AND MATE: Some colonies highly traditional—both natal and breeding philopatry (some breed away from natal colony). No opportunistic breeding (cf. great white and Australian). Rarely faithful to same site-mate; sub-colonies shift from year to year. Apparently no ‘non-breeding nests’ within colony.

AGE OF FIRST BREEDING: Not adequately known but 2-year-olds seen courting, copulating, and even feeding a young bird, but no evidence of successful breeding. Probably usually breeds at 3 or 4.

NON-BREEDING YEARS: No information.

LONGEVITY AND MORTALITY: Has lived at least 26.5 years in wild. Annual adult mortality not known. Estimated 41% mortality first year after fledging (Strait and Sloan 1974) seems unexpectedly low and annual adult mortality (estimate) of 21.3% for years 3–13 seems unrealistically high.

Brown Pelican *Pelecanus occidentalis*

PLATE 2

Pelecanus occidentalis Linnaeus, 1766, Jamaica.

Other common names: Peruvian or Chilean pelican refers to distinctive race *thagus*.

French: pélican brun, grand gossier. German: braun pelikan. Spanish: pelicano, alcatraz, alcatraz moreno.

Sub-species

Most variable pelican; 6 sub-species. Once referred to sub-genus *Leptopelicano* (Reichenbach). Current sub-species: *P.o. occidentalis* Linnaeus 1766, West Indies. *P.o. carolinensis* Gmelin 1789, Atlantic coasts of Americas from S Carolina to Orinoco.

P.o. californicus Ridgeway 1844, Pacific coast of America, California to Mexico; formerly also Galapagos form. *P.o. murphyi* Wetmore 1945, Colombia to N Peru. *P.o. urinator*, Wetmore 1945, Galapagos—said to be indistinguishable from Caribbean form (Swarth 1931). *P.o. thagus* Molina 1782, Peru and Chile; formerly specific rank—large, with well-defined, endemic range.

Description

ADULT M PRE-BREEDING: Upperparts pale ash or silver grey; feathers of back, rump, wing-coverts, scapulars edged blackish-brown; of upperparts

narrow and lanceolate; primaries black with much white on shafts; secondaries, tail-feathers dark grey-brown, 'frosted'. Underparts mainly brown. Feathers of flank and sides of breast with silvery shafts. Much of head, including small crest, straw-yellow though back of head and broad band of side neck at edge of gular pouch white; head of *californicus* and *carolensis* may be mainly white. Hind neck deep brown with chestnut or reddish hues. Nape feathers form chestnut mane. Facial skin lead, turquoise or cobalt blue. Eye light yellow but may be dark, at least later in breeding season. Eye-ring blue, pink or scarlet. Pouch vivid early in courtship; greenish or bluish-brown with orange-red area towards throat varying with individual; fades rapidly after pair-formation. Bill light grey-brown with blue, especially on lower mandible; may be spotted with red; bill-tip orange-yellow. Legs, feet black.

ADULT F: Similar but slightly smaller.

POST-NUPTIAL: Head and neck whitish with yellow tinge on head and base of fore-neck, a plumage acquired by moult but may be present in some birds (immatures?) at any time. Vivid colours of face and pouch fade after egg-laying.

JUVENILE AND IMMATURE: Mostly brown on upper-parts merging into white on breast; flanks grey-brown. Eye yellow-brown; bill, face dull grey-blue-brown; legs, feet grey-blue. In 2nd year head and neck fuscous, darkest on crown and sides of head. Back dark with paler parts grey-brown instead of silvery. Lower breast, rump, upper tail-coverts streaked black-brown and silver; underparts white, flanks brownish. Adult plumage acquired in (probably) 3rd or 4th year. Females generally assume adult plumage at younger age than males (cf. *solids*).

Field characters

Except for Peruvian race, which in non-breeding plumage is whiter on head and mantle, brown pelicans are unmistakably dark.

Measurements (see Appendix)

Huge differences between smallest race *occidentalis* and largest *thagus*, perhaps due to different

environmental conditions in different parts of extensive range. Variations related to differences in temperature of surface water, which affect prey.

Moult (GFA)

Breeding plumage acquired by partial moult (head and neck) this feathering in turn replaced after egg-laying. Primaries and tail feathers moulted serially, interrupted so that three generations of feathers coexist.

Voice

Harsh grunts; during display calls 'hrraa-hrra', low and hoarse, possibly by expelling air during wing-jerk. Chicks first give short 'bark', later rasping 'k-rr-r-rr'; piercing scream associated with feeding. Mechanical sounds include bill-clapping.

Range and status

(Figures 6.10, 6.11) Schreiber and Riseborough (1972); Schreiber (1976b); Schreiber and Mock (1988); Johnsgard (1993); Wilkinson *et al.* (1994).

Most abundant and only marine pelican, breeding on Pacific and Atlantic coasts of the Americas. On Pacific from S California and Baja California S along Mexican coast, Gulf of California, Bay of Panama (70,000+ adults in Pearl Island Archipelago—more than USA). S to Chile, with outpost in Galapagos. Gulf of California 17 colonies in mid-1970s; 6 contained 3000+ pairs. On Atlantic occurs from N Carolina to Florida, off Mexico and S to Belize or beyond (information sparse). Also on islands off Venezuela to Trinidad and Tobago. Breeds in Greater and Lesser Antilles though Caribbean brown pelican now endangered. Two small colonies on Cayo Cochino Pequeno is first breeding record on Caribbean coast of Honduras. On Atlantic coast of S America ranges to Guyana, Surinam and casually to Amazon estuary.

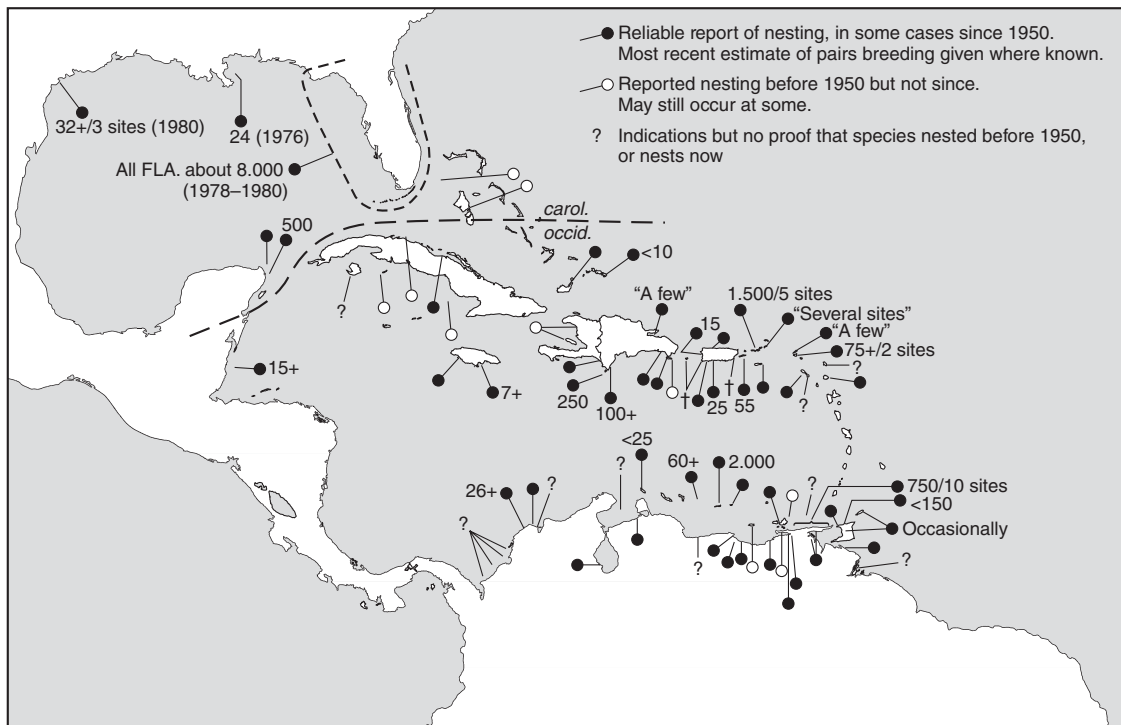
Pesticide poisoning caused precipitous decline 1950s–1960s in USA and Mexico; 40,000+ disappeared from Louisiana and Texas. Effects waning and Gulf coast population increasing although DDT and DDE residues still high in some areas, such as coastal Texas (King *et al.* 1985). For effects of DDE in eggs see Blus *et al.* (1997). World population substantial.



6.10 The distribution of the brown pelican. (After Johnsgard 1993.)

San Lorenzo Islands in Gulf of California held *c.* 32,000 breeding birds in 1970 although by 1977 only *c.* 8,200. Gulf of California and Pacific coast of Mexico in 1971, *c.* 30,900 pairs produced *c.* 50,000 young (Anderson 1972). In 1974, US Fish and Wildlife Service estimated that Pacific coast

colonies held *c.* 26,000 pairs and suggested *c.* 70,000 pairs for total US population. Although Florida and North and South Carolina populations considered stable since 1970 or (1980s) increasing, local populations may decline dramatically without this being evident statewide. Also censuses in other than



6.11 The breeding distribution of the brown pelican in the Caribbean (6200+ pairs). (From Halewyn and Norton 1984.)

month of peak-nesting (laying?) have potential error of 40–60% (Kushlan and Frohring 1985). But has recently expanded nesting range to Alabama, Georgia, Virginia and Maryland. On US Gulf coast nesting population more than doubled from 17 colonies (*c.* 5,600 nests) in 1970 to 31 colonies (12,700 nests) in 1989. On Atlantic coast increased from 8 colonies (2,800 nests) in 1970 to 27 colonies (13,700 nests) in 1991. On the E increased from 25 colonies (8,400 nests) in 3 states to 55 colonies (26,500 nests) in 9 states in 1989 (Wilkinson *et al.* 1994). Peruvian population (fraction of former) fluctuates but may exceed half-a-million breeding birds; *c.* 800,000 in 1981 including non-breeders (Duffy *et al.* 1984). In Caribbean thought to be 6000+ (2,300 in Puerto Rican Bank area). However, in Puerto Rico and US Virgin Islands (mean winter counts) 74% lower in 1992–95 than in 1980–82 and mean young per successful nest also lower; causes not known (Collazo *et al.* 1998).

Galapagos holds some thousands. World population 1,250,000+ seems possible.

Associates with Heerman's gull, in breeding range, dispersal pattern and foraging.

MOVEMENTS: Disperse or migrate for a variable distance (also inland), from more temperate to warmer latitudes, or remain more locally in tropical ones. Most recoveries (3,106 = 8.8% recovery rate) of ringed birds outside breeding season. Most fledglings leave nesting area during first months of independence. May wander extensively and remain in one locality for some time. Birds-of-the-year and those marked a year later, in Carolina, moved S and E to Florida, mean distance 600–700 km. Equivalents for birds marked in Florida somewhat shorter (*c.* 300–50 km and 250–80 km). Nestlings colour-marked in S Carolina and moving S and E, first sighted in Florida in Aug, about a month after fledging. Sightings increased to max in

Feb and dropped off sharply Mar–June. Florida-marked nestlings (Tampa Bay) sighted elsewhere in Florida in July, then about same numbers seen each month Sep–Mar, after which sightings declined. Many recoveries of ringed birds from Canada and USA in Cuba (Buden 1993).

Seems that food determines whether wintering individuals wander extensively. In America, E brown pelicans, especially more N ones, are truly migratory and adults travel as far S as young birds. In S Californian Bight post-breeding migration from Mexico augments local population during summer and autumn (up to 94,000 birds in Sep–Oct). Highest density occurred in warm, shallow water within c. 30 km of shore, though birds regularly occurred up to 75 km seaward of nearest island and up to 175 km from mainland. In autumn and winter adults predominated offshore, immatures along mainland shore (Briggs *et al.* 1981).

Foraging and food (GFA)

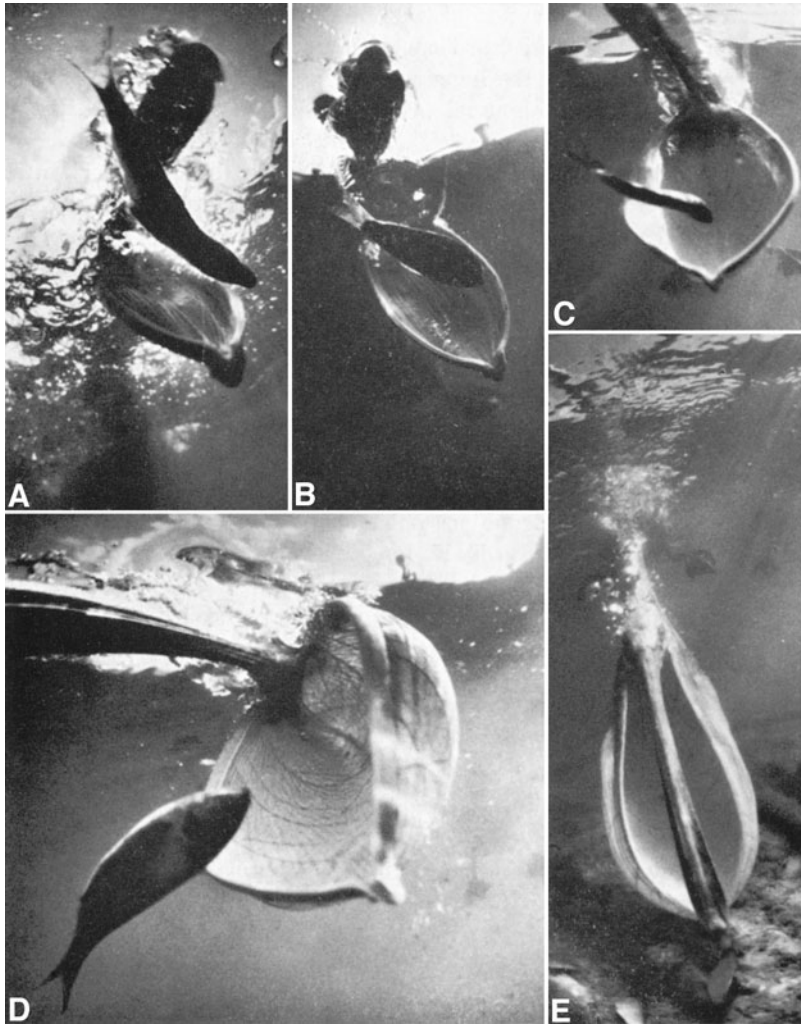
Commutes to and from feeding areas in small flocks, in files, or 'V's, flapping and gliding close to waves. Usually feeds inshore only tens of km from colony, singly or in groups but not cooperatively. Seen foraging 60 km from shore and off Peru reported further out to sea than boobies and cormorants. Densities 2–5 birds per km frequent in S Californian Bight and occasionally, near coast, 15+ per km. In Humboldt, off Peru, densities much greater.

Unique among pelicans in plunge-diving (Schreiber *et al.* 1975, details and photographs). Diving bird's trajectory constantly adjusted by altering angle of wing-tips. To correct to right or left body rotated but head stable to allow continuous sighting along bill, possibly concentrating on single fish. At instant of contact with water, legs and wings are thrust back. Bill enters water with pouch contracted and positioned so that target fish is between upper and lower mandible. Rami of lower mandible bend outwards to create a vast opening into expanded gular pouch, and water and fish pour in. Meanwhile upper mandible moves rapidly to close gap as lower rami return to normal position. Huge weight of water in gular pouch, more than weight

of bird, makes it impossible for pelican to manoeuvre bill. Tightly closed mandibles prevent fish escaping. Pelican disposes of water by raising head vertically; water flows out by gravity. Less than 2 sec elapse between hitting water and encircling fish, but up to a minute may be needed to drain pouch. May find difficulty in swallowing pouch contents; spill fish then pick it up again. Appears to minimize surface glare by orienting away from sun when diving. Dives shallow but strongly resemble sulids' in angle and wing-position, though initially neck more strongly kinked. Plunges from height of up to 20 m; often much less. Usually dives downwind and emerges into it. May 'scoop-feed' whilst swimming. Nixon and Lee (1998) found considerably higher feeding success (% successful dives) than brown booby in same locality. Feeds mainly in morning, but also at night. Radio-tagging showed one-fifth of each 24 hours spent foraging or feeding (Croll *et al.* 1986).

Although it seems they choose appropriate foraging areas, immature birds forage only 90% as efficiently as adults (Schnell *et al.* 1983). Coblenz (1986) suggests immatures less able to assess potential success of each dive. Actual diving skills probably equal in different age-groups. Carl (1987) reports that adults dive from greater height than juveniles or first-year birds but, oddly, adults and juveniles appear to use steep dives more than immatures. Carl reports lower success than previous observers; adults 14.4% (382), juveniles 7.9% (381).

More than 30 species of fish recorded as prey, overwhelmingly of no economic importance. Seasnake *Pelamis platurus* in diet off Columbia (Alvarez and Hernandez 1998). Breeding birds depend on abundant, local stocks of (often) particular species of prey. Anchovy *Engraulis* sp often dominate (sometimes, as in S Californian Bight, 1970–79 with *Engraulis mordax*, almost only food) and determine whether and how successfully the pelicans breed (Anderson *et al.* 1980, 1982). There breeders relocate each year, apparently in response to changes in distribution of food (Anderson and Gress 1983). In parts of N America the clupeid, menhaden *Brevoortia* sp, forms more than 90% of diet but elsewhere much less important. In Peru collapse of anchoveta *Engraulis ringens* has seriously



6.12 The use of the pouch in catching prey. (From Schreiber *et al.* 1975.)

harmful seabirds, including pelican. Anderson *et al.* (1978) maintain that brown pelicans do not compete significantly with commercial fisheries; entire population of pelicans in Gulf of California would consume less than one-seventh of fish thrown overboard from trawlers. At least 20 brown pelicans have died trying to swallow introduced S American sailfin armoured catfish (*Liposarcus multinotatus*) of Puerto Rico (Bunkley-Williams *et al.* 1994).

Will scavenge offal at sea and from shore outlets. Even as fledgling, may cannibalize smaller chicks.

Takes young guillemots (Thayer *et al.* 1999). Occasionally steals from other birds, especially cormorants, and is stolen from by e.g. roseate tern (Shealer 1996).

Habitat and breeding biology

(See Fig. at end of ch. 5; Schreiber 1976a, 1977, 1979, 1980.)

HABITAT: Typically marine. Gregarious—nesting, loafing, roosting, foraging, and migrating communally. On land, e.g. beaches, may roost ‘packed



6.13 A pre-breeding group of brown pelicans, Peru. (Photo: A.K. Kepler.)

shoulder to shoulder'. Prefers to breed on low, bare islands but will use coastal beaches or steep, rocky slopes. Peruvian race always nests on ground but others mainly in trees or shrubs. Especially mangroves (*avicennia*, *rhizophora* and *laguncularia*). But in Baja California and California, tree-nesting apparently unusual.

COLONIES: Traditional or may shift; as in other pelicans, prone to desertion after disturbance. Vary in size. Usually 50–500, range 10–1,500, occasionally 100,000+. N America (birds, not pairs): 1–50 (7), 51–100 (6), 101–200 (3), 201–500 (9), 501–1,000 (8), 1,001–2,000 (1), 2,001–5,000 (3) (Johnsgard 1993). Up to 15,000 nesting pairs Isla San Lorenzo, Gulf of California. Peruvian birds form largest colonies; Lobos Afuera \approx 200,000 birds (Murphy 1925), far fewer than on Coker's earlier visit.

In trees, nests in discrete units rather than random. Least distance between nests in mangroves at Tarpon

Key, Florida 1.3 m. Peruvian race \approx 2 nests per m² which, given their size, extraordinarily dense.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Northerly populations of *P. o. carolinensis* (30–5°N) in SE USA breed annually in spring-summer; at 20–30°N breed primarily in winter-spring; at 10–20°N breed over prolonged periods without clear seasonality. At all localities considerable spread of laying and significant variation from year to year. In N Carolina eggs laid mid-March–May (occasionally into late July); S Carolina mid-March–June; Florida late Nov–April (usually March–April) but at Tarpon Key (Florida W coast) nesting may begin Jan–Feb or even (one year) Dec. Breeding season showed tendency to become progressively earlier, 1971–76 by almost a month. Tarpon deserted Oct–Nov. Only 110 km S of Tarpon, colony in Charlotte Harbour began nesting early March for all recorded years. On

Florida E coast dramatic differences year on year with breeding sometimes beginning Nov (Schreiber 1979). Controlling factors not known. In tropical localities such as Galapagos or in Peruvian race may lay any month but least May–Sept. Environmental factors, principally climate and food (usually correlated) determine timing of laying. For example, pelicans of Bay of Panama nest only in dry season, associated with wind-driven seasonal upwelling and hence with food (Montgomery and Murcia 1982). In Antilles favour May–Sep. Often, laying not highly synchronized over colony as a whole. In any one year of Schreiber's study min 3 months and max 5–6 months separated time of first and last fledging. Thus young fledging from some nests whilst at others adults courting, building or incubating (Schreiber 1979).

No evidence that ever breeds more than once a year but not impossible that shorter-than-annual cycle may be endogenous although often (usually?) overridden by environmental factors. Peruvian race may have such a cycle, like other guano peleciforms. Successful cycle \approx 18 weeks; 1–2 for courtship and nest-building, \approx 4 incubation, 10–12 chick-rearing.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Once settled on potential nest-site male remains there except for brief circling flights. Serious overt fighting or contact rare. Territory defended by lunging and resonant bill-snapping. Ownership display 'bowing' confined to nest site.

Female selects male 'on-site', which means intruding onto it (a delicate balance). Where bonding rapid (a day or so) may simply be renewal of previous partnership. Male's display coincides with brief period of brightest bizarre nuptial colours and movement displays them to full effect. During pairing both partners 'bow', jerking their wings rhythmically and uttering a low, hoarse 'hrra-hrra'. They may then 'head turn', swinging it from side to side in a horizontal arc, punctuated by pauses and accompanied by intense eye-contact. They also 'head sway' (silent) and adopt an upright position with vocalization. Schreiber assigns following 'messages': head-sway—strong readiness to interact, both partners receptive and probability of attack or

escape relatively low; bow (site-ownership)—a tendency to attack (never to flee) if approached by bird other than mate; upright—somewhat ambivalent but may communicate fluctuating tendencies to remain or depart; head-turn—wide range of intensities and typically interspersed with other communication behaviour. Appears to signify readiness to associate, combined with marked appeasement component. Not strictly confined to nest-site or even breeding situation.

During pre-laying phase both birds frequently 'low-circle' nesting area.

COPULATION: (GFA)

NEST: If on ground, makes scrape with surrounding rim several cm high, or large mound, soil and debris. Cavity lined with few feathers. In Peru, scrape mere 25 cm diameter but this race nests especially densely, since food superabundant but nesting habitat limited. In trees or shrubs substantial nest of dead sticks, live branches, reeds, and other vegetation woven into supporting branches of tree. Nest material (such as living branches, sticks, and grass), gathered communally by males, who may denude entire areas. Material carried in bill though Peruvian race carries guano and sand in pouch (Coker 1919). Male 'presents' material by holding it for few seconds in horizontal bill with pouch distended, neck stiff and wings spread, before lowering it. Female builds and shapes cup by treading and body-contact. In trees, often mangroves,



6.14 Brown pelican collecting sand in pouch, Peru. (Photo: A.K. Kepler.)

building requires 7–10 days, though it continues, at reduced rate, through incubation and nestling stage. 5% of fully built nests failed to receive an egg (Schreiber 1979)—important when calculating productivity per nest.

EGG/CLUTCH: (GFA) $75 + 3.34 \times 19.95 \pm 1.32$ $n = 20$ (*P. o. carolinensis* Florida). Shell 0.510–0.579 mm thick. Shells 1969–70 approx 9% thinner than prior to 1943 (Anderson and Hickey 1970). Fat \approx 5% wet weight contents. Comparison of different races suggests somewhat separate gene-pools, possibly distinctive even for populations. Weight: *P. o. carolinensis*, Florida 98 g $n = 51$ (3.5% female's weight). *P. o. thagus* 133.6 (2.67% female's weight) $n = 9$. *P. o. californicus* 110.3 (2.9% female's weight) $n = 21$. Clutch 2–3; clutches 4 or 5 probably two females. Between 1969 and 1976 in Florida and excluding replacement clutches, mean clutch-size 2.62 (2.5–2.8) $n = 328$. In S Carolina adult-plumaged birds av 2.85 $n = 89$, whilst those with traces of immature plumage av 2.16 $n = 37$ (Blus and Keahey 1978). On Isla San Lorenzo Norte, Gulf of California, 1974–76, clutches av 2.88 $n = 305$, and among these, clutches of 3 eggs dominated (Keith 1978). 'Early' clutches in Florida av 2.5, 'middle' ones 2.6, and 'late' ones 2.2 (Schreiber 1979). Normal clutch requires 4–6 days and interval between successive eggs (at least 2 days but up to 64 hours) somewhat shorter than in those pelican species (and boobies) in which brood-reduction normal. Thus less age-difference between siblings. Fresh brown pelican eggs sometimes found on ocean beaches as result of 'indiscriminate' laying. Mostly laid early morning.

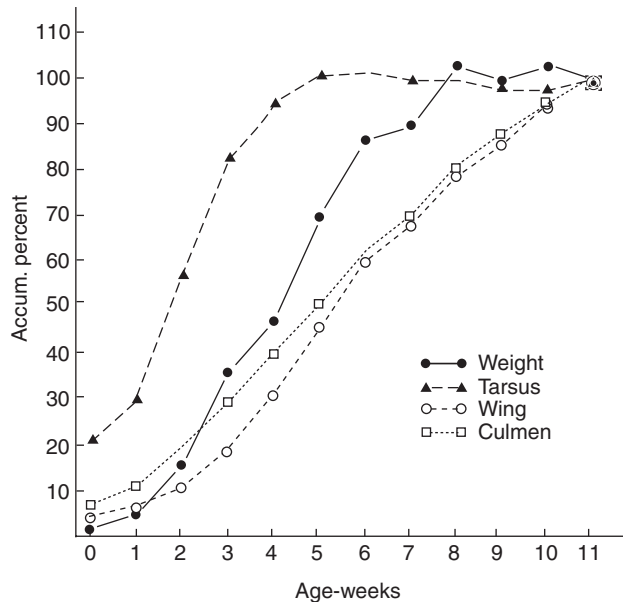
REPLACEMENT LAYING: Variable. None in 1970 but 26% in 1973 (Schreiber 1979). Occurs after loss of eggs or (rarely) nestlings. Clutches lost early in season much more likely to be replaced than later ones. 25 out of 30 nests in which eggs replaced had been started during first 4 weeks of season. Replacement clutch-size (2.5) same as initial clutch-size (2.4) but former fledged more young; reason unclear.

INCUBATION: First egg laid 1–3 days after completion of nest and requires 4–6 days; 24–72 hr between

eggs. Usually laid before 10.00 hr. Eggs incubated beneath webs except when hatching. Incubation period, \approx 30–31 days, shared by both sexes. Off-duty partner often remains near nest when not foraging. As incubation proceeds change-over becomes perfunctory.

CHICK/BROOD: (Schreiber 1976a) Hatchling 45–80 g, naked, pink with eyes open, though nictitating membrane inactive. Vocalizes frequently. Turns purplish 2–3 days and may crawl off nest if unattended. By day 8–10 egg-tooth disappears and movements become coordinated. Down appears on rump day 11–12 and on back a day or two later. By day 16–17 down on head less than 1 mm and neck still naked though body down 5–6 mm. Gular pouch, and with it gular fluttering as heat-regulator, develops whilst chick still downy. By day 21–23 primary sheaths measure 4 mm tipped with white down. Head covered with light-tan down; body down 10–20 mm. Neck down day 24–25 and scapulars erupt. Bill light greenish, feet pale. Chick can now stand or sit. Day 30–32 scapulars 25 mm; brown on back for first time; head grey. Day 35–37 longest primary reveals 35 mm of feather and 20 mm of sheath. Body down 25 mm. Day 45–47 tail feathers 30–35 mm long and scapulars \approx 90 mm. Weight more than doubles during weeks 1, 2, and 3; full weight achieved at 8 weeks when heavier than adult (if subjected to prolonged starvation can then grow rapidly, see Schreiber). Until about now has remained mostly on own nest-site unless disturbed. From \approx 60 days begins to wander; counts of young per nest become impossible. By day 62–65 wings clear of down and neck partly grey-feathered, rest downy. Down remains on rump, mid-back, lower neck, belly and axillas. Day 69–71 down remains only on flanks and under wings; still cannot fly. Day 72–75 down persists only under legs and wings; belly white, rest of body brown; some can fly, most remain near nest for few more days.

Brown pelicans rear more young per pair per breeding attempt than any other pelican with possible exception of spot-billed, which also arboreal. Although siblings compete damagingly for food and facultative siblicide occurs, 2 or even 3 young may be reared. Of those which died some time



6.15 Increase in weight and linear measurements of nestling brown pelicans, given as a percentage of the asymptote achieved prior to fledging. Asymptote taken as the mean of the combined measurements of adult male and female. (From Schreiber 1976a.)

after hatching, 74% were underweight, 55% bore peck wounds, and 43% had been displaced from nest (Pinson and Drummond 1993). First-hatched has greatest chance of survival. In broods of 2 or 3 first hatchling survived in all of 31 nests. By contrast, the 2nd hatchling in 3-chick broods died in 5 of 16 broods and fledged in other 11. In 21 2-chick broods, 8 died and 13 fledged. Finally, only 1 of 16 3rd-hatched chicks survived (Schreiber 1976a). Food deliveries decreased if brood experimentally reduced from 3 to 2; 'B' chick received less than 'A' chick, whose supply remained unchanged. 'A' and 'B' still competed and on av only 1 fledgling survived (Ploger 1997).

CARE OF YOUNG: (GFA) Shared. First feed may occur within few hours of hatching. During first 7–10 days adults regurgitate semi-digested fish into nest. Feed chick about once per daylight hour at this stage. Later feed from gape. Requires \approx 50 kg of fish to raise one young. After \approx 3 weeks close-brooding ceases but chicks guarded until 4–6 weeks, after which adults roost away from nest-site. Young rarely fed away from nest and then only when more than

10 weeks old. Because of differences in activity cycles mates may never meet at nest after chicks 5–6 weeks old.

BEHAVIOUR OF YOUNG: Small chicks pick up food in uncoordinated manner and swallow it unsteadily. At \approx 10 days beg actively and take food directly from adult's gape. At \approx 50 days begin to move from nest and before fledging may demolish it. Few details of behaviour during development or of sibling interactions, but since some pairs rear 2 or even 3 proves siblings more tolerant than some other pelicans.

FLEDGING: First sustained flight 71–88 days, mean varying with year 74–77 days. Do not return to nest and not fed by parents. (Does this apply to ground nesters?) At peak weight some chicks exceed adult but then lose some, mainly in 9th week.

POST-FLEDGING: Apparently not fed; young that can fly properly do not return to nest and adults do not accompany them.

BREEDING SUCCESS: (Schreiber 1979) Hatched from laid: 53–89%, overall 70.9% ($n = 860$, Florida,

6.16 Reproductive success in brown pelicans. (From Schreiber 1979.)

	<i>Early nests</i>	<i>Middle nests</i>	<i>Late nests</i>
Nests	104	189	35
Eggs laid	265	497	78
Clutch size	2.5	2.6	2.2
Eggs hatched	223	351	34
Nests in which eggs hatched	84	155	27
Hatching success	84%	70%	43%
Young fledged	88	208	22
% eggs produced fledged young	33	41	28
% hatchlings produced fledged young	39	59	64
Successful nests	68	131	15
% successful nests	65	69	43
Fledglings per successful nest	1.3	1.6	1.5
Productivity (fledglings per total nests)	0.8	1.1	0.6

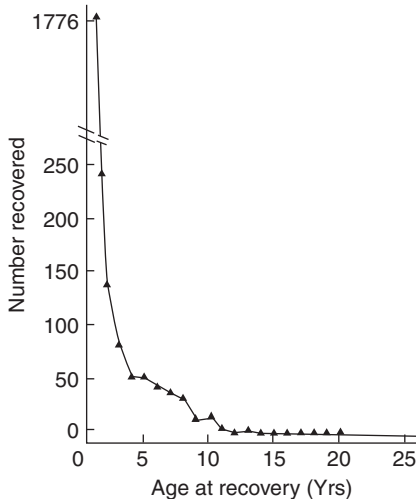
1969–76); 74.3% ($n = 669$) from 3-egg clutches against 27.8% ($n = 18$) from 1-egg clutches but later likely to be from younger birds; 84% early eggs and, to lesser extent mid-season eggs, significantly higher than late-season, 43%. Fledged from hatched: 16–77%, overall 37%. Oddly, fledging success highest (64%) for late nests, lowest (39%) for early. Less surprisingly, highest in single-chick broods. Fledged from laid: Figure 6.16. Schreiber (1979) gives details. Fledged per pair: ≈ 1 per year but varies—0.33–1.69. Fledged per successful nest: 1.48 (1.0–1.74). Peak-season nesters most productive (1.1 per nest; 0.8 for early; 0.6 for late). Experienced females raised 0.89 fledglings against 0.11 for inexperienced. Latter nested later, laid smaller clutches and had lower hatching success. In Puerto Rico, fledged per successful nest dropped from 1.65 (1980–82) to 1.14 (1992–93) (Collazo *et al.* 1998).

Failure due to: tidal flooding; pesticides; tourist disturbance, scientists, photographers, fishermen; and possibly to tick-infestation among dense ground-nesters, especially Peruvian race. Young sometimes starve (Kushlan and Frohning 1985). Predation not

significant if undisturbed. Only Schreiber has properly investigated effects of disturbance by investigator and found it resulted in fallen eggs and reduced hatching success but apparently did not affect success of those chicks that did hatch. Birds habituate to routine and non-invasive disturbance.

FIDELITY TO COLONY, SITE, AND MATE: General area used in successive years though recruitment from areas outside may occur, e.g. birds fledged outside S California Bight moved in and bred (Anderson and Gress 1983). Precise nest-site of individual pair not known to be regularly re-used. Similarly, pair-bond probably usually for one season though if site retained possible that partners may reunite.

AGE OF FIRST BREEDING: May vary with area and age-structure of colony, between 2 and 4 years. Seen breeding in immature plumage and known 2-year-old found incubating. At a new colony in Louisiana birds first nested when nearly 3 (Williams and Joanen 1974). Schreiber and Mock (1988) give 3 years and an effective reproductive lifespan for



6.17 Recoveries, by age, of brown pelicans ringed as nestlings (or in year of hatching) in Florida (n = 2519). (From Schreiber and Mock 1988.)

most adults of only 4–7 years. Anderson and Anderson (1976), however, say most may not breed successfully until 4–7, yet very few live longer than 10 years. Adult colouration achieved

3–5 years, females earlier than males (probably typical in core peleciform families).

NON-BREEDING YEARS: No information. Certain to occur in Peruvian population during El Niño years but whether rest-years are a normal feature of lifetime reproductive strategy is unknown.

LONGEVITY AND MORTALITY: Only 30% of ringed nestlings survived first 14–15 months and fewer than 2% known to live more than 10 years. Nevertheless, potential longevity much greater; ages of 31, 37 and 43 years recorded. Old rings can be lost. Annual adult mortality estimated *c.* 18% and first-year mortality 70–75%, but figures highly provisional. Recoveries of brown pelicans ringed in Carolina and Florida 1925–83 indicate 8.8% recovery rate, though this cannot be translated into mortality rate. Use of mortality rates in computations of productivity necessary to maintain stable population needs caution. Henny (1972) suggests that each breeding female would need to produce 1.5–1.87 young per breeding attempt to maintain stable population.

Gannets and Boobies

Australasian Gannet *Morus [bassanus] serrator*

PLATE 3

Sula australis Gould, 1841, Tasmania. G.R. Gray first used *Pelecanus serrator* for specimen taken in 1769 off Three Kings Islands, which is therefore the correct type locality (Medway 1993).

Other common names: Australian gannet, solan goose.

French: fou Austral. German: Australtöpel.

Spanish: alcatraz Australiano.

Sub-species

Allo-species of superspecies *Morus bassanus* (see Atlantic gannet).

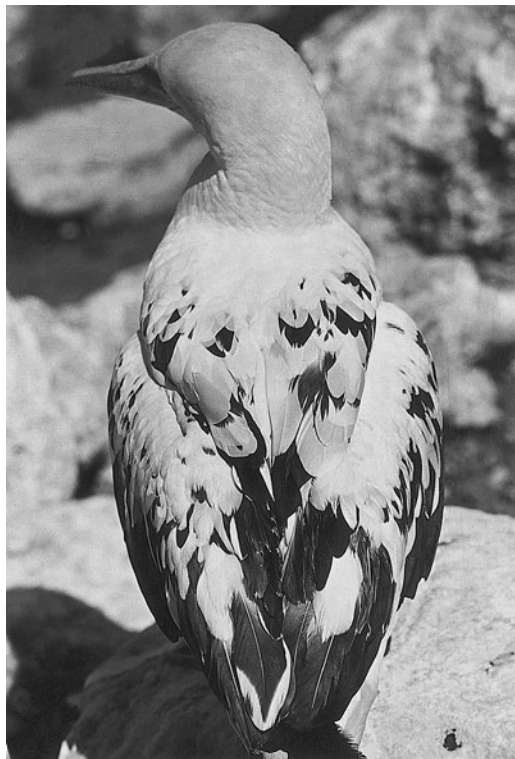
Description

ADULT M PRE-BREEDING: Large; snow-white body plumage; black primaries, most secondaries (proximal three white). Black trailing edge of wing thus stops \approx 12 cm short of body. Primary coverts usually black, may contain some white. Humerals, scapulars, tertials white. Alula black. Tail, usually 10 or 12 feathers, white except (usually) 4 central blackish but variable; 3–10 black feathers, outer 2 always white. Often, 1 or 2 variegated feathers separate white from black (see Broekhuysen and Liversidge 1954). The 4 black centrals with 4 white on each side does not indicate a more mature bird than one with variegated feathers. Head and neck golden buff varying with season. Bill and face as in Atlantic and African with black gular strip much as former. Orbital ring and eyelid bright blue, iris grey-blue, darker



6.18 One-year-old female Australasian gannet. Note that, as in the Atlantic gannet, she is behind the male in plumage development. (Photo: C. J. Robertson.)

than Atlantic. Often, distinct narrow band of dark pigment encircles pupil. Legs, feet blackish grey with conspicuous greenish lines varying between blue and yellowish along tops of toes and up tarsi.



6.19 One-year-old male Australasian gannet. (Photo: C. J. Robertson.)

ADULT F: As male.

POST-NUPTIAL: As pre-breeding except head paler.

JUVENILE AND IMMATURE: Juvenile markedly whiter beneath than Atlantic, with fewer but larger white spots on back and wings, giving paler appearance than most juvenile Atlantics. Do not usually acquire boldly pied pattern of 2nd year Atlantic but move to adult plumage via more finely variegated intermediates though with some large splashes of black and white. Also, mature plumage acquired more rapidly. A 9-month-old bird had head, neck and underparts as adult, dorsal surface blackish-brown variegated with white, considerably in advance of any Atlantic gannet of that age. Stein (personal communication) says black on body and wings nearly gone by end of first year. Serventy *et al.* (1971) claim adult plumage attained in 2 years but this does not apply to most. Two birds, exactly



6.20 Two-year-old Australasian gannet. (Photo: C. J. Robertson.)

2 years after ringing as chicks, had lost dark body plumage but retained many dark covert feathers. Generally attains adult plumage at 4 years (ringed birds, Robertson, personal communication).

Field characters

See Atlantic and African. Australasian closely resembles African but has much shorter black gular stripe (skin), darker iris and usually 4 black central tail feathers (range 3–10), whilst African usually has all black tail (but significant variation). Gular stripe about same length as Atlantic's but iris much darker.

Measurements (see Appendix)

Voice

Distinctive 'urrah-urrah' but male voice markedly higher pitched than female—even squeaky or 'yappy'. Special vocalization 'yorr' accompanies sky-pointing. Individual variations in voice more obvious to human ear than in Atlantic; clear that

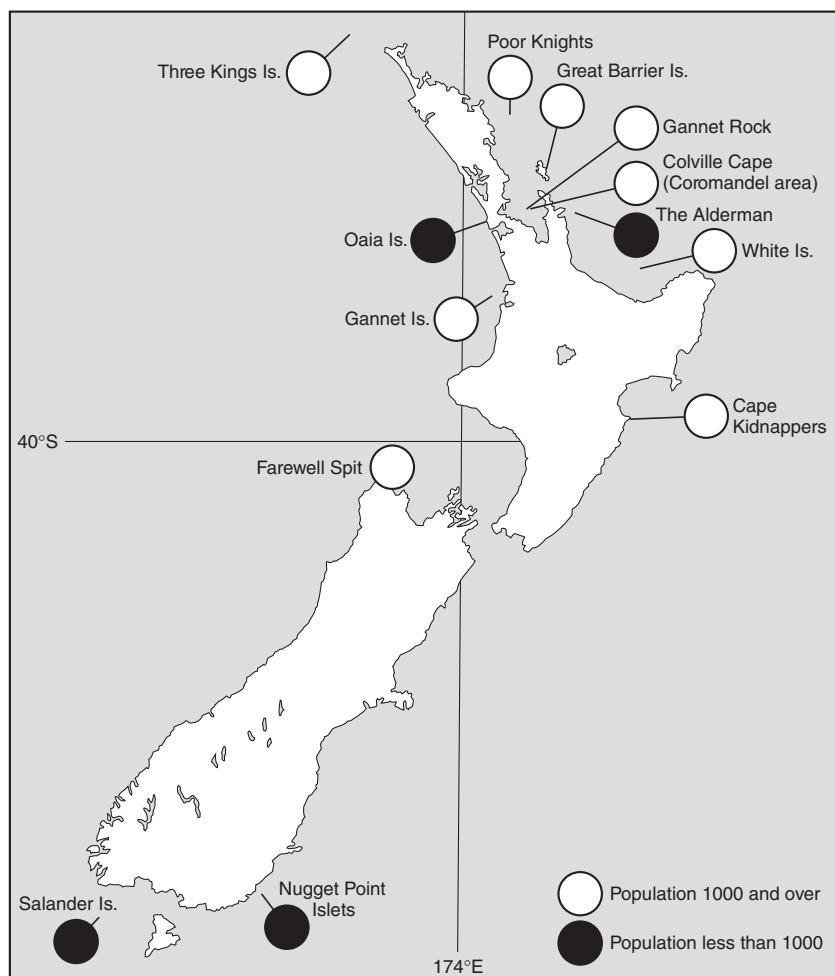
individuals recognize each other. Noise of colony a high-pitched gabbling in which rapid, frenetic and rising-pitch calls of inflying males conspicuous.

Range and status (Figure 5.16)

Second rarest sulid after Abbott's booby; present population >70,000 pairs and could be 73–75,000. Increasing after former low. Breeding range 32°12'–46°36'S but more than 99% breed between 34°–40°S. Occurs mostly in temperate waters from sub-tropical to sub-Antarctic zones, thus, as with other two gannets, relying on cool, productive waters. Northernmost New Zealand gannetries at Three Kings Islands and southernmost on Little Solander near Foveaux Strait. If colony status

accorded to every separate group there are 37 colonies; Cape Kidnappers would count as 3 (now possibly 4). But this merely demarcates sub-groups. If adjacent groups counted as one colony, 28 New Zealand gannetries, plus 6–8 (most extremely small) in Australia–Tasmania. Even this total arbitrary.

Stronghold is E seaboard of New Zealand S to Hawkes Bay. In 1980/81, 99% nested in colonies around N half of North Island. A colony at Muriwai (Auckland) increased from 28 pairs (1975) to 1,393 pairs (1998) (Greene 1999). New colony Farewell Spit (South Island) established *c.* 1981 at sea level and subject to wash-out (see Hawkins 1988; Cook 1997). Consists of 3 groups, 2 further subdivided. In Nov 1993 aerial count 1,947 nests;



6.21 The distribution of colonies of the Australasian gannet in New Zealand. From: Nelson (1978b)

in 1994, 1,843 nests, and in 1995 *c.* 3,000 birds. In 1997 *c.* 1,000 pairs in 6 groups (Heinekamp, personal communication). Immigrants include birds ringed as chicks on White Island.

National census New Zealand 1946–47 indicated *c.* 21,000 pairs; 1969–70, *c.* 37,800 pairs; 1980–81, *c.* 46,000 pairs. Mean annual rate of increase over 34 years 2.3% (Wodzicki *et al.* 1984) similar to that of Atlantic. Since then, Cape Kidnappers has grown and Farewell Spit become established making New Zealand total >49,000 pairs. If one adds probable increase at other New Zealand gannetries since 1981 census, present population in New Zealand perhaps *c.* 53,000 pairs. To this estimate must be added possibly 2000 non-breeding individuals for various colonies.

Australian and Tasmanian colonies (Figure 6.22) mainly new, small, or both, though Cat Island (Tasmania) ancient and once a major gannetry and Black Pyramid now substantial at >12,000 AOS (Bunce *et al.* in press). 1980–81 estimated 6,660 pairs nested in Australian waters (Wodzicki *et al.* 1984). Present total >23,000 AOS; Bunce *et al.* (in press) give *c.* 20,000 breeding pairs, representing an increase of 6% per annum. 1986–87 aerial photo of main Victorian colony, at Lawrence Rocks, 2,463 pairs (a few bred Port Phillip Bay); estimate 3,000+ breeding pairs in 1993 (Norman and Menkhurst 1995); aerial photo of 5,490 \pm 150 adults Dec 1993; *c.* 6,200 birds Dec 1996 (Fisher and Cooper cited in Norman *et al.* 1998).

Wedge Light (artificial platform) first nests 1966, 58 by 1996–97. Pope's Eye, established *c.* 1985 partly by Wedge Light birds, increased to *c.* 162 pairs (115 chicks ringed) in 1996–97. In that year, of 39 ringed adults, 29 had been ringed as chicks at Pope's Eye, 5 at Wedge Light, and 2 at Lawrence Rocks. In 1990s at least 3 groups nested on navigation piles, Port Phillip Bay (29 chicks on one, 15 on 2nd, 24 nests on 3rd—1997). One bird had been ringed as a chick at Wedge Light. Began breeding at Point Danger (*c.* 6 km from Lawrence Rocks) 1996–97 but eggs broken (*c.* 150 birds, 6 broken eggs). Aug 1997 *c.* 450 birds; nest-building and copulation.

An adult *African* gannet paired with an Australasian at Wedge Light in 1981 and has since bred

most years, producing offspring which paired with Australasians there. Interbreeding occurred also at Lawrence Rocks; in 1993 4 birds, in 1994 7 adults and 2 chicks. This coincided with discovery of attempted breeding of both 'species' on St. Paul Island (IO) roughly midway between their respective breeding areas and *c.* 4,000 km outside normal range (Lequette *et al.* 1995). Observations during 14 visits 1986–93 revealed an African gannet 1987, 1991 and Australasian in 1988, 1989, 1991, 1992, 1993. Up to 13 individuals (species not recorded) in 1986. Up to 10 Australasians noted 13–15 Dec 1988 along with 1 egg and 1 chick (found dead 14 Dec). Whether single African gannet recorded was same individual on different occasions not known. No evidence of mixed pairing. Australasian has been recorded in African gannetry (Berruti 1988).

Spread of Australasian gannet compares with Atlantic gannet—both attributable to cessation of persecution and thus increase in recruitment. If Australasian gannet increased throughout 20th Century (Fleming and Wodzicki 1952), rate of increase nevertheless quickened in last 20–30 years, to about 2.8% per annum. Now increasing at some established colonies and forming new ones.

MOVEMENTS: Juveniles migrate up to 5,000 km W or NW across Tasman Sea; exact parallel to distance travelled by other two gannets; like their's, migration is from cool to warmer water (Figure 6.19). Whilst juveniles from Cape Kidnappers may move N or S (mainly N) Horu Horu birds almost all move N. Some, when clear of land, turn S, thus initially moving in opposite direction to eventual passage; again like other two. Probably on wing by time begin to cross Tasman, which can do at *c.* 400–possibly 800 km per day. Indicates similar urgency to reach target offshore-area as in several seabirds with extensive migration.

Juveniles disperse widely over coastal waters of E Australia, covering nearly 22° latitude (2,480 km) and taking northernmost birds into sub-tropics. Also considerable movement along Australia's S coast. Some travel up W coast as far as 28°45'S, *c.* 12,000 km from origin (Horu Horu). Juveniles from this colony appear to fall short of Kidnappers birds in extent of movement up E coast, hinting at somewhat different though overlapping ranges.

6.22 World population of the Australasian gannet.

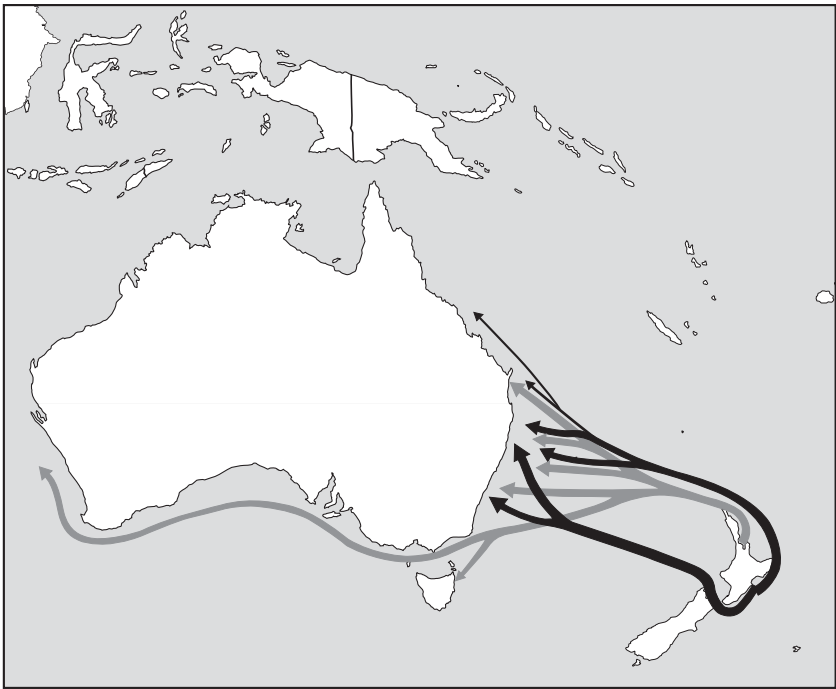
<i>Location</i>	<i>Last count and year (AOS★ or pairs)</i>	<i>Comment</i>
Australia		
Black Pyramid	12,339 (1999)	First count (900) 1961
Pedra Branea	3,013 (1999)	500–1,000 (1978)
Eddystone Rock	189 (1999)	46 (1978)
Nepean	6 (1978)	
Phillip Island	4 (1980/81)	
Cat Island (Tasmania)	6 (1983/84)	Once populous
Wedge Light (Port Phillip Bay)	507 (2000)	68 nests 1996/97
Pope's Eye	162 (1996/97)	Additional platform 1989
Lawrence Rocks	6,200 (1996/97)	
Point Danger	600 (1999/2000)	First roosted 1995
Australian Sub-total: 23,026		
New Zealand		
Three Kings		
South-west Island	1,135 (1980/81)	} Photos in 2000 show population increase
Hinemon Rock	4,136 (1980/81)	
Hole-in-wall	1,530 (1980/81)	
Tutanekai Rock	402 (1980/81)	
Arbutus Rock	2,652 (1980/81)	
Poor Knights		
High Peaks Rocks	1,553 (1980/81)	Photo in 2000 shows increase
Sugarloaf Rock	2,017	Photo in 2000 shows increase
Mokohinau Islands		
Cathedral Rocks	344 (1980/81)	
Great Barrier Islands		
Mahuki Island	2,681 (1980/81)	
Colville		
Double Island	96 (1980/81)	
Bush Island	3,530 (1980/81)	
Motutakapu	925 (1980/81)	
Horuhoru	2,647 (1980/81)	
Moriwai		
Oaia Island	761 (1980/81)	
Muriwai Stack	298 (1980/81)	
White Island		
West Point	1,550 (1980/81)	
Rocky Point	1,257 (1980/81)	
Gannet Point	3,986 (1980/81)	
Kanhia		
Gannet Island	8,003 (1980/81)	

* AOS: Apparently occupied site.

6.22 *Contd.*

<i>Location</i>	<i>Last count and year (AOS or pairs)</i>	<i>Comment</i>
Tolaga Bay		
Moutara Rock	611 (1980/81)	
Cape Kidnappers		
Black Reef Rocks	2,500 (1986/87)	Spread onto mainland
Saddle Colony	2,200 (1986/87)	
Plateau Colony	1,800 (1986/87)	
East Beach	c. 800 (2000)	C. J. Robertson (pers. comm)
Marlborough Sounds		
Otago	33 (1980/81)	
Fovaux Strait		
Little Solander Island	62 (1980/81)	
Farewell Spit	800–1,000 (1996/97)	Variable; very low success
N.Z. Sub-total: 48,509		
Total: 37 Individual locations 71,535 AOS or pairs		

Notes: 1. Aerial survey (2000) indicates N.Z overall numbers increasing though some colonies may be stable. (C. J. Robertson, pers. comm.). Total population (rough estimate) now 55,000 ± 2,000 pairs.



6.23 Supposed migration routes of Australasian gannets ringed at Horuhoru (→) and Cape Kidnappers (→) (New Zealand) and recovered in Australia and Tasmania. Terminal arrows indicate limits of recoveries. (After Wodzicki and Stein 1958.)

Occasionally reaches South African waters and one recently recorded for Namibia (Dyer 1995). Paterson and Riddiford (1990) mention (no reference) an Australasian gannet reaching Brazil.

Immatures remain in Australian waters, mainly off E coast south of Capricorn and in Bass Straits for 2 or sometimes 3 years (extremes 1–4) but recoveries of 4th-year birds in this area extremely rare. Evidently birds in 3rd year leave Australian waters and arrive in gannetries. Birds in 1st year seldom, and 2nd year uncommon, at breeding colonies. Some 1st-year birds seen around New Zealand may have remained there since fledging, just as a few 1st-year Atlantic gannets remain in home waters.

Most breeders remain in New Zealand coastal waters outside breeding season, though one recorded back in Australian waters, just as occasional adult Atlantic gannet returns to African waters.

Numerous watches off New South Wales up to 60–70 km offshore (well beyond Continental Shelf) recorded gannets all year round, mainly 1–30 km offshore.

Foraging and food

Feeds mainly within *c.* 40 km of shore, principally on surface shoaling fish. Opportunistic; some species found in only a few samples and in only 1 or 2 out of 5 seasons. However, 84% of 667 regurgitates from several colonies contained only 1 prey species (Robertson 1992); he calculated 2.4 feeding trips per pair per day. Feeding methods as other gannets and similarly takes fishery discards. Food-load up to at least 400 g and up to 23 items per regurgitation. Av regurgitation at Motu Karamarama 259.3 g and at Cape Kidnappers and Gannet Island 245 g, though at Port Phillip only 46 g (Norman and Menkhurst 1995). A free-living gannet's daily food requirements estimated 20% body weight or 270 g. Individual prey-items up to 30 cm. Wingham (1985) reports 77% prey 11–20 cm. At Port Phillip av 14 cm. At Pedra Branca took mainly pelagic shoalers, especially redbait *Emmelichthys nitidus* (72% by number and 56% by mass) and jack mackerel *Trachurus declivis* of length less than 20 cm (Brothers *et al.* 1993). At Port Phillip 58.4% prey pilchards *Sardinops neopilchardus*, 72% less than 14 cm (again 82% regurgitations contained only 1 prey

species). Cape Kidnappers and Gannet Island main prey pilchards, anchovy *Engraulis australis*, saury *Scomberesox saurus*, jack mackerel and squid *Notodarus* sp (Robertson 1992). But these two gannetries differed greatly in composition by weight of their prey.

Brothers *et al.* compare gannets' diet with commercial species, where jack mackerel principal target and redbait a by-catch. Mean size commercial fish of both species greater than that taken by gannet, thus apparently excluding direct competition. Energy requirements of an entire colony of gannets and thus food consumption estimated by Wingham (1989); large potential disparities between direct (empirical) calculation and modelling.

Extensive prey spectrum; 34 species of fish, more than two-thirds offshore shoalers. At Port Phillip 20 species fish recorded and 4 cephalopods. Main prey pilchards but also barracouta *Thyrasites atun*, garfish *Reporhamphus ihi*, sardine *Sardinus neopilchardus*, flying fish *Cypselurus* sp, horse-mackerel *Trachurus novae-hollandiae*, mullet *Aldrichetta forsteri*, needle fish *Scomberesox forsteri*. Squid *Notodaurus sloanii* and *Mendosoma lineatum* less than 1% of mass overall but in some months up to 6% (Wingham 1985).

Total weight of prey caught by entire population of Australasian gannets in New Zealand calculated (in tonnes): pilchard 2,880, anchovy 2,020, saury 2,140, others 1,840 (Robertson 1992).

Habitat and breeding biology

(See Fig. at end of ch. 5; Australasian, Personal observation, Wodzicki and McMeekan 1947, Warham 1958, Wodzicki 1967, Stein 1971, Robertson, 1985.

HABITAT: Like African, Australasian largely flat-ground-nester, on tops of offshore islands and rocks and, occasionally, mainland headlands. Ledges used, as on Poor Knights, are broad and flat. Atlantic gannets thus unusual in choosing precipitous cliffs.

COLONIES: May be large and dense; av between nests 79 cm (70–87), similar to Atlantic but less dense than African. Maximum density of long-established groups 2.59 nests per m², minimum 1.68, compared with max for Atlantic 3.53 and African *c.* 6 nests



6.24 Colony of Australasian gannets. Note synchrony in age of chicks, dense nesting and sharp edge to colony.

per m². May establish new nuclei, separate from main group; loose assemblage of pre-breeders, perhaps accustomed to roost there, slowly coheres into nesting group and compacts. May eventually fuse with main colony. New breeding colonies likewise preceded by roosts. Like other two gannets, nesting groups have clean edges which, with regular spacing of nests, characterizes gannets. Some colonies grow by immigration.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually. Spends 6–8 months at breeding colony; av 190 days (Waghorn 1983). Arrives N colonies around July, month earlier than S colonies. Return date highly variable; Cape Kidnappers birds may be present by 3rd week June or not until Aug. Seasonal breeder showing marked synchrony within sub-groups but considerable spread over colony; peak laying varies year to year. Over entire range, first eggs July and last Dec, Jan

or even Feb; 8-month span, though not at any one colony. Earliest recorded egg 12 July 1959 at Horu Horu, about 4–5 weeks ahead of Kidnappers. Difference at least equal to Atlantic gannets at British E versus W coast colonies. At any one gannetry laying spread over 15 weeks, about same as Atlantic gannet. Kidnappers first egg usually late Sept (some years late Oct) and last late Dec. Peak laying date (Kidnappers) often mid-Oct but varies up to 3 weeks. Incubation and growth of chick av 145 days and mean fledging date varies from c. 10 March to several weeks either side, according to colony and year. At Kidnappers, almost all chicks fully feathered by early Feb. Within colony, significant differences in timing of different groups; peak laying 20 Nov in one small group (Kidnappers 1967) but 26 October in a larger group (age/experience not known).

TERRITORIAL AND PAIR-INTERACTIONS: Qualitatively identical to other two but differs from

Atlantic in frequency and intensity of aggressively motivated behaviour and more closely resembles African (significant in ability of these two to interbreed) which it closely resembles in size and plumage. Territorial fighting frequent but short and mainly due to mis-landings. Robertson (personal communication) notes prolonged territorial fighting which can prove fatal. Ritualized threat frequent; extensive movement of wing-tips and tail, which flick up behind head. Whether mere balancing or exaggerated (ritualized) movement which conspicuously displays black and white tail unclear but movement much more extreme than in Atlantic. Compared with Atlantic, site-ownership display at typical intensity contains fewer head-dipping movements (redirected aggression) and wings not held so high, but context and function identical to Atlantic and African. Males bow more frequently and at higher intensity than females.

Ritualized nape-biting of female by incoming male, significantly less frequent than in Atlantic or African (less than 10% against 98% and 97%).

Greeting ceremony (mutual fencing) typically shorter and lower intensity than Atlantic though may be intense and prolonged and is important reinforcer of pair-bond. Typically followed by mutual preening.

Skypointing differs from Atlantic and African. Context (pre-movement, usually pre-departure) as for others and upward straining of head and neck and 'on-the-spot' lifting of drooped webs also similar. But Australasian moves head slowly up and down, as does African but not Atlantic. Folded wings swivelled at humeral joint so that wing-tips move up, as in Atlantic but lacks high wing-raising of African. After this posturing, loosens wings and bounds upwards with wheezing call. Sky-pointing, though signalling departure from site, does not inhibit neighbours' aggressive response and birds from central sites dash for fringe rather than passing through nesting ranks in skypointing posture.

COPULATION: (GFA)

NEST: Compacted guano and detritus though may contain vegetation—often seaweeds of at least 8 sp such as *Carpophyllum plumosum* and *C. maschalocarpum*—and local ground flora. Plastic



6.25 Sky-pointing; a ritual at change-over to co-ordinate nest relief.

debris (81% from fishing activities, mainly cordage) also used (Norman *et al.* 1995 record it in 34.5% of nests, Lawrence Rocks). Nests often substantial enough to raise egg or chick above substrate—important in heavy rain which can kill many chicks. Male gathers material and flies or walks back with it. Pilfering common and nest usually guarded continuously.

EGG/CLUTCH: 77.57 (67–88) × 46.97 (43–50) n = 200; 76.8 (65–89) × 46.6 (35–53) n = 710; 78.55 (69.35–85.21) × 47.70 (40.46–51.19) n = 175. Weight: 99.8 (84–125) n = 135, or *c.* 4.1% female weight (assuming av 2,400 g early in season); significantly more than Atlantic (3.4%). Replacement eggs wider but not longer than 1st eggs (48.50 ± 1.14 against 47.63 ± 1.54) Port Phillip (Norman and Menkhorst 1995).

Evans (1995) found egg-surface temperatures little affected by ambient temperature. During first 4 days incubation 34.9°C increasing thereafter to 36.5°C. Internal temperature of pipped eggs *c.* 1°C higher due to embryo heat. Surface temperature of eggs *c.* 2°C below deep adult body temperature (40.3°C). Heat probably transferred from body through feet.

About one in thousand nests contain 2 eggs; lower proportion than in African, probably due to lower nests of latter, which thus displace more eggs to be rolled in by a neighbour. No genuine 2-egg clutches recorded.

REPLACEMENT LAYING: Common (e.g. 68/162 or 42% Port Phillip) if eggs lost before Dec; 3rd egg

sometimes laid. Often 'considerable period' between 1st and replacement.

INCUBATION: Shared; period 43–4 days. Stints (Tasmania) \approx 27 hr (24 hr 57 min; 26 hr 32 min; 30 hr 40 min). Mean surface temperature of egg 34.9°C, first 4 days, increasing and stabilizing at 36.5°C. Internal temperature \approx 1°C higher. Adult deep body temperature 40.3°C (Evans 1995).

CHICK: Hatchling 60–70 g, black and naked. Down 1 cm long by week 2, much longer by week 3, by which time chick may be left fully exposed. By week 4 too big to be adequately covered. Attains adult weight 6–8 weeks; max \approx 3,250 g or 130–40% adult weight, similar ratio to that in Atlantic gannet. At week 7+ primaries and tail-feathers appear. At week 9 chick half-feathered and prone to leave nest for periods. Completely clear of down around week 12 but may remain at colony for up to further 3 weeks. Wing feathers not fully grown until 15.5 weeks. At 14 weeks wings still 10 cm shorter than adult's. Length of tail feathers surprisingly constant and may be used to age chick within 3 days. Despite smaller size, development slower than Atlantic gannet.

Several pairs given extra young, none reared twins (Robertson personal communication) (cf. Atlantic gannet).

CARE OF YOUNG: After initial close brooding, chick generally guarded for 6–8 weeks. Av brooding spell 12 hr 43 min (9–18+ hr). Later, brooding spell averaged \approx 5 hr. Resembles African gannet in that mid-to-large young often unattended thus releasing adults for simultaneous foraging. May be linked to much reduced tendency (compared with Atlantic) for adult (male?) to attack unattended young. Indeed, Australasian adult may allow neighbouring young to 'visit'—impossible in Atlantic gannet. Feeding frequency av twice per day. Wodzicki and Robertson (1953) claim that, once having left nest, young may be fed at colony by adults other than their parents.

BEHAVIOUR OF YOUNG: From \approx 6 weeks chicks may wander, tendency later becoming marked.



6.26 Chick beak-hiding from attacking adult—probably an intruder. (Photo: J. Warham.)

Nest-occupying chicks strongly resist intrusion by others, but may interact, sparring with, and even preening other young. If attacked by adult, young lie prone or hide bill beneath body in appeasement.

FLEDGING: Chicks from 30+ days may leave nest and join groups on fringe (Norman and Menkhurst 1995). This behaviour, which did not occur Cape Kidnappers 1978–79 (personal observation), probably due to disturbance. When 8 or 9 weeks, chicks wander through colony and exercise wings. Later, many go to fringe, jump, wing-flap and make short, wind-borne flights like ground-nesting boobies. Some return to nest towards nightfall or when parent returns. In this resemble African gannet but differ markedly from Atlantic. Thus, on departure many Australasian youngsters capable of sustained flight. However, entails longer fledging period and loss of fat, which alters balance of selective forces acting on juvenile and may necessitate more rapid passage to target area. But increases options for Australasian and in this more akin to ground-nesting boobies.

Fledging period 95–103 \pm 3 days (Warham 1958) defined as leaving Cat Island (not merely nest); 107–9 at Horu Horu (Stein 1971); 93–115 Cape Kidnappers (Robertson 1985).

POST-FLEDGING: Young not fed after leaving the colony to go to sea.

BREEDING SUCCESS: (Horu Horu, Stein 1971; Cat Island, Warham 1958; Cape Kidnappers, Wodzicki and Stein 1958, and Robertson 1985; Port Phillip, Norman and Menkhorst 1995.) Hatched from laid: 98% (n = 1350, Horu Horu); 91% (n = 18 Cat Island, heavy rain can cause loss); 45.7% (n = 459), 31.2% (n = 208), 60% (n = 150), 65% (n = 100), 0 (n = 35), 6.5% (n = 31), Cape Kidnappers, but these figures take no account of, obviously considerable, disturbance; 64% (n = 384, 5 seasons, Port Phillip, loss partly due to tourists and poor nests with subsequent dislodgment of eggs). Fledged from hatched: 94% (n = 17, Cat Island); 90+% (Cape Kidnappers, 6 years); 89% (Port Phillip, 1985–91); 44.4% (n = 840, Horu Horu 1949–50). Violent rain can cause heavy loss; estimated 80% mortality by Christmas, Horu Horu 1952. Small young starve as heavy weather prevents adults feeding—140 dead chicks in 3–6 weeks, Horu Horu, 1949. Fledged from laid: 70+% (variable between years and colonies); 57% (Port Phillip, 5 seasons). In 1950–51 only 250 fledged from c. 1500 breeding pairs and in 1951–52 only 208. In both years almost all survivors older chicks. In every year 1954–57 inclusive, 900–1,000 chicks fledged from Horu Horu. At this colony fledging success occasionally less than 10%; no known parallel in Atlantic gannet. Probably lower in new groups and sub-optimal locations. Thus colony at sea level on Farewell Spit has lowest recorded success of any gannetry. One group seems never to produce fledglings and in 1994, in entire colony of >2,000, only 66 chicks available for ringing (Heinekamp, personal communication). Storms can cause great destruction (e.g. Cook 1997). At Port Phillip little difference in success in relation to orientation, though some indication more exposed nests fared less well.

FIDELITY TO COLONY, SITE, AND MATE: Having once bred, remains faithful to colony for life. Natal philopatry evidently strong but pre-breeders liable to join expanding group which may not be natal one, though within overall ambit of colony. Thus Black Reef Rocks at Kidnappers received many recruits from main Plateau colony which in turn received recruits from Saddle group. Although less than 0.5% of birds reared on Plateau recovered

elsewhere, this depends on searching effort. Return to colony increasingly after 2 years, but often not until 5th or 6th year.

Fidelity to site and mate apparently strong. Stein's study suggests lifelong fidelity and Robertson's long-term data (personal communication) concur.

AGE OF FIRST BREEDING: Wodzicki (1967) records most birds ringed as chicks back in colony in 4th year (57 of 276 sightings) or 5th (101 of 276). Two-year-olds (3rd year) rare (Cape Kidnappers). At Horu Horu one bird aged 1 yr 4 months recovered at colony. Apparently does not breed until 4th–7th year. Of 23 birds recovered in 5th or 6th years 9 were breeding, 14 were in 'clubs'. Seems most birds lay in 6th year. However, Wodzicki and Stein (1958) say 'at the age of 6–7 years only about half the birds are breeding' and Stein (personal communication) that often they first breed at 6–8 years. Robertson states that in young pairs female generally at least year older than male, which (oddly) reverse of tendency in Atlantic gannet. Seems Australasian gannets do not breed (or attain adult plumage) as young as Africans. Conceivably, the large number of birds known to be older than 5 but apparently not breeding are failed breeders.

During Dec–Jan large numbers of slightly immature gannets arrive at Cape Kidnappers (earlier at colonies further N), much as peak numbers of immatures present at Atlantic gannetries in June–July.

NON-BREEDING YEARS: No information.

LONGEVITY AND MORTALITY: 21 years recorded. Stein (1971) calculated that some birds live 37–42 years (some of his assumptions may be invalid). Annual adult mortality 4.5%, based on large sample ringed birds Cape Kidnappers and Horu Horu. Assuming 75% breeding success, pre-breeding mortality of 85% (65% 1st year, 10% 2nd, 5% 3rd and 4th), a pair breeding for 20 years would produce 2.25 recruits. On these figures, population would increase around observed rate of 2.8–3% per year.

Of 45 recoveries in 1st year of life 51% fledged 2–6 weeks previously; 88% recovered within 9 weeks of fledging. Of 28 recoveries for which cause of death known 14 died after storms, 10 trapped in

nets or on hooks, remainder shot or oiled. In Australia, juveniles seen coming ashore in heavy surf, probably weakened by starvation. New Zealand Beach Patrol Scheme (Powesland and Powesland 1993) found 5,637 gannets, 1943–91, av 6.49 per 100 km of coastline; 24.1% in adult plumage, 5.4% in juvenile plumage, remainder

plumage unrecorded. Recovery rates increased more or less in parallel with population increase. Peak period of adult mortality (whether breeders not known) Dec–Feb, in peak chick-rearing period.

‘Wrecks’ occur; in 1995, 648 birds recovered on New Zealand coastline at av rate 22 birds per 100 km (Taylor 1997).

African Gannet *Morus [bassanus] capensis*

PLATE 3

Dysporus capensis Lichtenstein, 1823, Cape of Good Hope.

Other common names: Cape gannet, malagash or margout, kolonjane.

French: fou de Cap. German: Kaptolpel. Spanish: alcatraz del Cabo.

Sub-species

Allopecies of superspecies *Morus bassanus*. Usually treated as full species *Morus capensis*. ‘It is not a very interesting question whether at present North Atlantic and Cape Gannets form one or more geographic species, or, for that matter, form the members of one superspecies. What is far more interesting is what has caused the greater intra-specific aggression in the North Atlantic gannet’ (Voous 1980); the question I raised (Nelson 1963, 1965).

Description

ADULT M PRE-BREEDING: Large; snow white body plumage; black primaries and most secondaries, though black trailing edge to wing stops several cm short of body. Primary coverts black but humerals white. Tail usually all black but may have 1 or 2 white outer tail feathers; 14 different combinations of white and black tail feathers recorded from 3,682 birds (Broekhuysen and Liversidge 1954). Head deep golden buff, bill and facial skin as in Atlantic gannet but black gular stripe noticeably longer c. 13–19 mm. Eyelid bright blue; iris typically darker than light grey-blue of Atlantic. Legs, feet blackish with light greenish yellow lines along toes and up tarsi.

ADULT F: As male but gular stripe said to be shorter (Jarvis 1971).

POST-NUPTIAL: Little change. Presumably head colour pales as in Atlantic gannet.

JUVENILE AND IMMATURE: Newly feathered juvenile identical to some Atlantic though white spots on underparts typically more conspicuous. Immature stages variable, as in other gannets; progression to adult plumage may be quicker than in Atlantic.

Field characters

(See Atlantic) Main diagnostic features in adult African is combination of all black tail and black secondaries stopping several cm short of body, and long black gular stripe (hard to see in flying birds). Faster, shallower wing beats and shorter glides of African compared with Atlantic reliable only when 2 species seen together. A few 3-year-old Atlantic gannets may conceivably retain all black secondaries (usually white with 1 or 2 black). Even then confusion unlikely unless Atlantic bird retained mainly or completely black tail (unlikely). Some immatures may be impracticable to separate. Australasian has shorter gular stripe, darker iris and usually just 4 black tail feathers. May overlap with masked booby (white head, black mask, and all black secondaries).

Measurements (see Appendix)

Larger and heavier than Australasian; smaller and much lighter than Atlantic.

Voice

Similar to Australasian and less strident than Atlantic. Male higher-pitched than female. Same range and context of vocalizations as other two.

Range and status (Figures 5.16 and 6.27)

Whilst Atlantic and Australasian gannets increasing for several decades, African now increasing in South Africa but declining in Namibia. Jarvis's (1970) study showed downward trend in guano since 1940s; circumstantial evidence links possible decline with development of inshore fishing industry and deliberate culling.

Breeds from 25°43'–33°50' S and from 14°50'–26°17' E. Even narrower range than Australasian and (now but not formerly, Abbott's booby excepted) most limited breeding of any sulid. But recently noted in breeding attempt with Australasian gannets on St. Paul's Island (IO) (Lequette *et al.* 1995) and successfully interbreeding in Port Phillip Bay. Range influenced by proximity of food-rich Benguela current, thus resembling other 2 gannets in its association with productive areas. Possible, that as in Peruvian booby and Humboldt, other seabirds associated with Benguela may limit space available for breeding gannets.

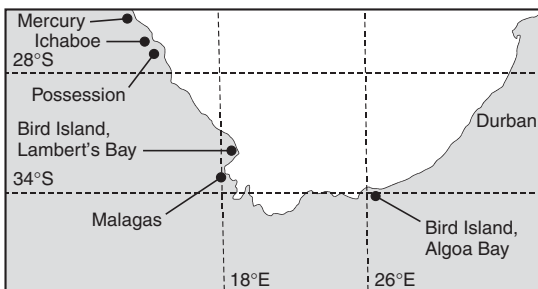
6 colonies (Figure 6.28): South Africa—Bird Island (Lambert's Bay), Malagas, and Bird Island (Algoa Bay, currently growing at *c.* 2.8% per annum, Klages personal communication). Numbers increased 1953–96 at all three South African colonies. Namibia—Mercury Island, Ichaboe, and Possession; all three have decreased (1978 population only 52% of 1956 and there was a 31% decline 1956–96). Comparison of counts (individuals) in South Africa and Namibia—332,400 (1956), 353,000 (1963), 177,000 (1967), 186,000 (1978), 346,000 (1996)—indicate decrease followed by

some recovery (Nelson 1978b, Crawford and Shelton 1981, Crawford 2000). Initial decline followed decrease in pilchards and recent increases possibly due to increase in anchovies. Past counts/calculations questionable. Present totals based on calculations of breeding pairs derived from area covered. African gannet probably now totals >350,000 individuals (many more than Australasian but fewer than Atlantic) but the decline in Namibia may begin operating in South Africa in the near future (Crawford 2000).

MOVEMENTS: non-breeding range extends north to slightly beyond equator on western side of Africa and offshore for several hundred km. A gannet ringed Algoa Bay, Feb 1985 recovered alive off W Australia Oct 1986, distance of 7,877 km. Also recent overlap with Australasian in S Indian Ocean, where previously neither known to occur. Recently accepted record of African gannet off Argentina (Bergkamp 1995) but no mention of diagnostic gular strip. Extreme southerly record Beagle Channel, Tierra del Fuego (Ramirez 1996).

African gannets may occur European and British waters. Old record (MacGillivray 1852) from Bass Rock correctly identified but rejected because doubt about whether acquired there. Recent (1985–87) spate of sightings off Spanish coast (Paterson 1987; Paterson and Riddiford 1990; Mackrill personal communication) but adult seen by Mackrill 30 km east of Tarragona (Spain 40°40' N, 01°17' E) 28 Jan 1985 only record accepted by International Record Committee. Identification difficult. During sea-watches off Land's End, Mackrill saw 6 gannets with all black secondaries and mainly black tails and photographed one. Large movements of African gannets into European waters would be notable discovery.

Juveniles and immatures occur off African coast everywhere S of equator, reaching Gulf of Zanzibar and occasionally Mombasa on E and throughout Gulf of Guinea on W (Jarvis 1971; Brown *et al.* 1982). Adults mostly remain within *c.* 500 km of breeding areas; of 99 birds ringed as adults on Malagas, 71% <540 km away but 17% >1,460 km—greatest 2,700 km, 3,380 km. Adults leave colonies May–July and move along W



6.27 The breeding distribution of the African gannet.

6.28 World population of the African gannet.

<i>Colony</i>	<i>Area (ha.) covered by breeders</i>	<i>Approx. number of breeding pairs</i>	<i>Year</i>
Lambert's Bay (South Africa)	0.34	c. 5,350 ? (5,000) 14,000	1956 1971 1996
Malgas Island (South Africa)	2.10	c. 21,000 >54,000 71,000	1956 1958 1996
Bird Island (Algoa Bay, South Africa)	2.40	17,884 70,000 68,000	1956 1994 1996
Mercury Island Namibia	0.05	c. 5,000 c. 1,000	1956 1996
Ichaboe Namibia	0.56	c. 100,000 c. 18,000	1956 1996
Possession Island Namibia	0.02	Reputedly c. 13,000 but 16,924 also cited and used here 750	1956 1996

N.B. The 1956 totals for entire population differ according to source.

- Notes: 1. In 1996, total population, breeding pairs, c. 173,000 of which 153,000 (88%) were in S.A. and remainder in Namibia.
2. Exchanges between breeding localities mean that neither S. African nor Namibian populations are 'closed'.
3. Annual adult mortality c. 7% (Crawford 1999).
4. Mean age of first breeding, 4 years (Crawford 1999).
5. Density of nests 0.8–4+ pairs per m².
6. Populations estimated from area covered.

African coast though some occur off E. Ringed birds recovered N of equator in Rio Muni, Cameroon, and Nigeria, and occurs off Ghana. At Cape Lopez and Point Gentil first gannets, nearly all juveniles and immatures, arrive mid-June but month later adults far outnumber immatures, many of which have moved on. At Point Gentil many adult gannets arrive when water cools and depart when it warms. May be tendency to follow cooler water. Davies (1956) correlated restricted movements on SE and E with pursuit of migrating pilchard *Sardinops ocellata*.

Juvenile's northward migration closely parallels migration of other two gannets, taking it 2,000–4,000 + km northwards to equator, as Atlantic

migrates southwards to equator, where two mingle. Most northerly recovery of ringed (1st-year) African gannet 21°40' N in Canaries Current. Broekhuysen *et al.* (1961) showed newly fledged gannets move mainly to Angolan and W African equatorial coastal waters, though recorded recoveries may be biased due to more Europeans on W than on E; juveniles certainly move up to 4,000 km on E coast. But juveniles from E coast colonies may move up W, migrating S before turning N; some Atlantic gannets migrate N before turning S.

Juveniles which leave colonies about April reach N regions by June. Many remain there for at least a year, returning to natal colonies mainly in 2nd or 3rd years. This long migration perhaps takes

inexperienced juvenile into waters with more readily available prey (different species, size, and density, perhaps more evenly distributed).

Foraging and food

70% forage within 50 km of coast, which coincides with purse-seining area—fishery removing same species as gannet. Further out, gannets benefit from discards of deep-water stern trawlers. Prey spectrum permits switch from depleted prey, as for instance on the W coast of South Africa, where pilchards and horse mackerel replaced in gannet's diet by anchovies, non-shoaling pelagic fish and trawler discards (Cooper 1984). Berruti *et al.* (1993) monitored species composition at Lamberts Bay and Malagas (1977–89), and demonstrated significant differences between them in seasonal preponderance of main prey. They associated presence of hake (trawler offal) in gannet's diet with lack of shoaling fish inshore. Later (1989–91) when biomass of Cape anchovy declined gannets took more sardines. But overall 1984–92 tolerably good relationship between numbers of gannets on Bird Island, Lambert's Bay (as measured by area occupied) and biomass of spawning Cape anchovy which fluctuated between 0.5 and 1.75 m tons (Crawford and Dyer 1995).

Feeds on at least 20 fish species and on cephalopods. Crustacea and polychaetes found in gannets probably from fish stomachs. Pilchards in 35% of stomachs, forming 51% of diet by weight (up to 652 g in one stomach) ($n = 257$ adults shot up to 15 km offshore). 63% pilchards 5–20 cm long. Maasbankers in 17% of stomachs, formed 20% of diet by weight and 62% 6–10 cm long. Equivalent figures for anchovies 13%, 12%, 5–13 cm long. Cephalopods in 19% of stomachs but formed only 2% of diet by weight. Klages *et al.* (1992) found squid, mostly *Loligo reynaudi*, formed av 0.6% (0.1–9.7%) by numbers, 3% (1–16% by frequency of occurrence and 1.6% (0.2–13.6%) by mass. Davies (1955) 98 stomachs, found pilchards 50% of diet by weight, maasbankers 16%, anchovies 11%, mackerel 16%. Where a few species abundant shoalers, gannets concentrate mainly on them but elsewhere compensate by taking variety of prey. Pilchards rose to 94% of diet by weight in Aug and

main prey for 9 months of year, including winter months of June and July. In some years maasbankers main prey. Reasonable meal $c. 350$ g; birds that quickly locate enough fish will not feed again that day. But Jarvis found hungry captive given unlimited food ate av 752 g of pilchards at a meal. Presumably depends on interval between feeds. Rarely eats theoretical max— $c. 839$ g (Rand 1959). Daily intake slightly more than 13% adult body weight. After 3 hours half food ingested disappeared from stomach. After 40 hours assimilation complete (cumulative excretion of carmine dye ingested with meal reaches 100%; Laugksch and Duffy 1986).

Habitat and breeding biology

(See Fig. at end of ch. 5; Jarvis 1971)

HABITAT: Breeding islands few, crowded, hot, and flat (Figure 6.24) though will use cliffs, as on Mercury Island. Will nest on man-made structures.

COLONIES: Large, but will breed in small groups. On Bird Island, Lambert's Bay, nearly 5,000 nests in 2,400 m², av density 2.05 pairs per m² (Jarvis 1971). He gives max density 8.6 nests per m²—physically impossible at $c. 4$ times density of Atlantic gannetry? On Ichaboe $c. 4.2$ nests per m² (430 in 1,000 ft², Rand 1959) where breeding island approached saturation, but down to 0.8 pairs per m² on uneven, rocky areas. Assuming that in low-density areas nests not clumped (measurements excluded topographically impossible ground) such wide range of nesting densities not paralleled in Atlantic gannet.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually. Colonies occupied mainly late Aug–late May; most adults disappear when chicks fledge. Some attended as roosts by some, mainly male, adults (no immatures) throughout non-breeding season. Varies with year; colonies may be entirely deserted May–July. June 1956 only 15 gannets on Malagas, June 1957 almost as many as in summer. As in Atlantic gannet, adults return with extensive fat deposits. One male weighing 2,752 g in Aug had 106 g perivisceral fat, another (2,892 g) 114 g (Jarvis 1971).



6.29 Colony of African gannets. (Photo: J. P. Strijbos.)

Lays early Oct–late Dec, peaking around first half Nov, total laying period \approx 90 days. Rand (1963a) gives April as latest month for laying, indicating extreme range—greater than Atlantic gannet. Fledges mainly March but many April–May. Some indication that peak eggs most successful, producing chicks which grow during period of optimal food. Post-fledging mortality heavy and may provide selection pressure for timing of breeding via extrinsic factors such as weather (heavy seas) and accessible food. Recoveries indicate heaviest mortality in late fledgers.

Synchrony can be marked but not extreme—for example from onset of laying mid-Oct–23 Nov, 82.5% nests $n=120$ had eggs and of these, 62.5% laid 25 Oct–15 Nov. This rate of laying slightly slower than Atlantic gannet. Very considerable spread on Ichaboe (25 Nov 1985); thus of 360 nests, 3.9% empty, 31.1% contained eggs, 62.5% naked or downy chicks and 2.5% feathered young (Crawford *et al.* 1986).

Total length breeding cycle \approx 24 weeks including pre-laying attendance \approx 1 month. Latter considerably shorter in Atlantic gannet and since, in addition, African lacks post-breeding attendance, total time of 24 weeks at colony compares with 35–8 weeks in Atlantic. Difference may relate to lower premium on defence of site in African and reduced role for social stimulation in timing of breeding.

Morphology, ecology, and behaviour resembles Australasian far more than Atlantic. The behavioural differences between the African and Atlantic gannets illustrates the wide ranging effect of their apparent difference in aggression (see Nelson 1978a).

TERRITORIAL AND PAIR-FORMATION: Interactions qualitatively and contextually extremely similar to Atlantic gannet. Territorial fights (same sex only) av 5.4 min (longest 15 min) and probably less extreme than in Atlantic (max \approx 2 hr). Post-landing aggression redirected to ground or nest virtually

absent whereas in Atlantic male common. Threat display 15 times less frequent than Atlantic. Ritualized territorial display, 'bowing', in African less frequent and extreme in form and in expression of aggressive component. Thus territorial aggression lower in African gannet although breeding sites probably fewer. Social factor in site competition probably more important in Atlantic than in African.

Greeting (aggressive component) shorter and lower intensity than Atlantic.

In other details of territorial and pair behaviour two gannets seem identical. They 'flight-circuit' before landing, vocalize as fly in, 'prospect' similarly, and male nape-bites female but not vice versa.

African (not Atlantic) gannets often land at site in dark. May relate to less danger for lighter bird landing on flat ground than for heavier bird landing on cliff ledge and perhaps to less severe consequences (attack from neighbours) of mis-landing.

Males 'advertise' sexually, and females 'prospect' for a mate similarly to Atlantic. Initial contact between sexes often results in attack from male. Often, female approaches male in half sky-pointing posture. In response to attack may present her nape (facing-away). After initial pair-formation incoming male African bit female on 97% of occasions $n = 319$, identical to 98% of Atlantic gannet and much higher than in Australasian ($<10\%$). Incoming female attracted bites on 60% of 130 cases compared with 75% in Atlantic. Although female African does face-away (appeasement) in anticipation of, or response to, male aggression, she occasionally retaliates (*contra* Atlantic) by gripping male's bill in booby-fashion (male Atlantic's threshold for aggression is lower). Much behaviour of African and Australasian nearer to boobies than is that of Atlantic gannet.

Greeting ceremony (mutual fencing) lasts av 58 sec during courtship phase; less than one third as long as Atlantic gannet's. Less often followed by pair-bonding 'kiss-preening'. Copulation less prolonged and seasonally less protracted. All suggests weaker pair-bond.

'Skypointing' preceding departure from site, distinct from Atlantic gannet's. In African low-intensity form closely resembles high-intensity form of Atlantic but with frequent dipping movements of

head, absent in latter (but present in Australasian). But at higher intensities African assumes postures quite different from northern bird. Wing movements continue beyond tip-lifting stage until, in extreme position, lifted high. At about mid-point in range, looks as though slight rotation would produce wing-swivelled position of blue-footed booby's sexual 'advertising' display (Figure 6.41) but African continues to lift wings upwards until high above back. Simultaneously, upward-pointing of bill takes head backwards of vertical. Gular strip expanded 2–3 times normal width.

Thus, from common beginning (slight lifting of wing-tips probably as intention-movement of flight) movement has become a wing-swivel in some sulids, resulting in high lift of wing-tips, or, at most extreme, rotating the wings so backs face forwards (see blue-footed booby). Only in African gannet has it continued as straight lift of wings—neither a swivel nor a horizontal spread.

Neighbours reacted aggressively to sky-pointing, by threatening or pecking, on 35% of occasions, a higher aggression-eliciting score than that of other behaviours of comparable physical magnitude (fuller discussion in Nelson 1978b: 260). Jarvis showed that males skypoint more frequently than females (consistent with fact that they leave nest site more often) and that it precedes copulation. Latter of particular interest since, in boobies, skypointing has become sexual advertising display. Evolutionary sequence for this functional change speculatively: skypointing precedes movement for nest material; mutual nest-building precedes copulation; sky-pointing comes directly to precede copulation and so becomes linked to sexual activity and becomes sexual advertising.

COPULATION: (GFA)

NEST: Scrape or collect guano and debris from immediate neighbourhood. Deposit by mandible vibration and head-shaking. Nest-touching and handling common displacement behaviour during pair-interactions. On Malagas av nest weight 1770 g. Experimentally demonstrated (Jarvis 1971) that birds lay earlier and are more successful when nest large, presumably because birds older and experienced.

Earlier fledglings heavier than later ones and may be expected to survive better. Although seaweed not used in construction of nest, it is not scarce. Possible that use of guano arose from habit of excreting onto feet to regulate body temperature.

EGG/CLUTCH: 76.13 (64.8–85.2) \times 48.22 (42.6–48.2) $n=100$; 80 \times 51.3; 78.85 \times 48–50. Weight not recorded directly but measurements imply that it constitutes 3.9% of female weight compared with 3.4% for Atlantic gannet. Difference accords with slower growth and longer foraging stints of African gannet. 34 of 44 eggs laid 12.00–07.00 hr, mainly 12.00–15.00 hr. Of 1,337 nests 1.05% contained 2 eggs (Jarvis 1971) but no evidence any genuine 2-egg clutches.

REPLACEMENT LAYING: Of 41 pairs that lost eggs before end Nov 18 re-laid and a further 18 probably did. Of 16 pairs that had eggs removed on 14 Dec, only 1 re-laid. 6 eggs lost when 1-day old replaced in 12 days (2), 15 (2), 16 and 24 days. 2 lost when 2 days old replaced in 2 and 25 days. Remainder as follows: lost at 6 days replaced after 20; 7 (20); 11 (30); 18 (24); 22 (27); 23 (26); 23 (27); 27 (27); 28 (20–55). 3 females laid 2 replacements taking 22, 18–23 and 21–26 days respectively to replace it for the second time (first replacements had taken 24, 14–15 and 16 days).

INCUBATION: 42–6 days (mean 44). Pipping to emergence $c.$ 36 hr. Male incubation shifts during first half incubation av 45 hr, female's 38 hr; during 2nd half, 43 and 40 hr. Overall av 41.3 hr compares with 32.9 for Atlantic gannet, consistent with slower growth of African, indicating further or longer food-foraging.

CHICK: Development (Figure 5.27) slower than Atlantic gannet (Cooper 1978; Navarro 1992). Peak weight $c.$ 80–90 days (56–70 in Atlantic) thereafter decreasing slightly. Max weight $c.$ 3,190 g some 109% adult weight (max 4,000 + g up to 140% adult weight in Atlantic). Growth and therefore presumably food varies between years.

For age-related changes in fat and non-lipid contents of various body parts of chicks, juveniles and adults see Navarro (1992). Fat content of muscles,

internal organs, and integument increases from early in growth to fledging. Weeks 1–5 use energy mainly for development of organs, skeleton, and muscle, and weeks 5–10 for feathers and fat deposits. Final stage sees little development and chicks usually lose weight. Fasting capacity increased exponentially up to 70 days. Fat deposits of chicks 30–40 days could supply energy needs for 2–4.5 days; for chicks 50–70 days fat would last 6–16 days. Juvenile has paler underparts than Atlantic though very variable.

Jarvis (1974) duplicated my twinning experiment (Nelson 1964) with Atlantic gannet. His artificially twinned broods produced 19–46% more fledglings than normal nests but twins grew considerably more slowly and, unlike Atlantic, marked disparity arose between siblings; one about normal weight, other underweight. Fledging period 99 days twins, 97 singles and av fledging weight 2,544 g twins, 2,895 g singles. Since in normal singles lightweight fledglings seem to survive less well than those of av weight (of 24 recoveries, 13 a few km from colony, 11 much further, former had weighed 2,604 g at fledging, latter 2,930 g), it seems that as little as 10% difference in fledging weight might affect survival. In this case both twins but especially lighter ones would be disadvantaged. It remains unproven but perhaps unlikely that greater number reared would offset greater likelihood of dying. By contrast, in Atlantic gannet both twins fledged at near-normal weight and with correspondingly equal (to singletons) chances of survival. This reveals much about differences between these two gannets and, predictably, places African nearer to single-chick boobies in its limited capacity to rear twins.

CARE OF YOUNG: After hatching, attendance spells shorten to M 28 hr, F 31 hr (days 1–20); 18 hr, 19.5 hr (days 21–40); 18 hr, 16 hr (days 41–60); 13 hr, 11 hr (days 61–80); 10 hr (both sexes, days 81–100).

After $c.$ 45 days, chicks intermittently unattended. Some unattended from $c.$ 30 days, when sulids become capable of thermo-regulation. Atlantic gannets guard chick continuously from hatching to fledging. Length of unguarded spells in African 7–12 hr, often overnight. May imply need for greater foraging time than in Atlantic.

BEHAVIOUR OF YOUNG: Significant tendency to stray from nest (tolerated by adults) after *c.* 7 weeks and when fully feathered may form small groups on fringe, playing and performing mild threat, but may return to nest to be fed. This booby-like behaviour (found also in some pelicans) practicable on African gannet's flat-ground habitat and impossible on cliffs, but even on flat ground Atlantic chicks prevented from wandering by aggressive adults. Behaviour of African youngster may reduce dangers of fledging since can regulate food intake after 'mock' fledging and gain experience of wind at colony edge.

FLEDGING: Fully feathered young may spend days wing-exercising in fringe (cf. ground-nesting boobies), losing weight because not fed. Of 74 birds weighed at intervals, 38 consistently decreased in weight (max loss 425 g in 6 days). Some return for feeds; one fledgling lost only 85 g in 6 days. Av fledgling 2,900 g on leaving nest (not necessarily colony) compared with adult weight of *c.* 2,650 g. Fat reserve represents fuel. Navarro (1992) says 2 fledglings had sufficient for 4–8 days but ignores cost of flying and swimming. 15 shot, an estimated 'few' days from fledging, weighed 2,977 g (Rand 1959) which (oddly) exceeds weight given above for birds just leaving nest. Fledglings of very different weights survived to breed. Some fledge by jumping and swimming away, most fly. On two occasions, newly fledged youngsters actually flew back to island (Jarvis 1971). Juvenile's ability to fly far obviates danger of landing close inshore. African gannet's fledging more booby-like than Atlantic gannet's.

Fledging period 97.2 days (93–105) *n* = 15, compared with 90 days for larger and heavier Atlantic gannet.

POST-FLEDGING: Young not fed after fly fully.

BREEDING SUCCESS: Hatched from laid: variable; 85% (*n* = 55, 1966–67); 60% (*n* = 40 1967–68, low because nest material (guano) removed). Fledged from hatched: 96.9% (*n* = 129 chicks hatching in first half of 1966–67 season). On Ichaboe in 1985 more than 400 chicks, mostly downy, died in

abnormally heavy rain (Crawford *et al.* 1986). Fledged from laid: *c.* 74%, some years much lower. Rand claims eggs and young may be deserted, which smacks of food scarcity.

FIDELITY TO COLONY, SITE, AND MATE: 80% of birds ringed as adults subsequently recovered in same discrete group as ringed; many chicks return to colony of birth (Broekhuysen *et al.* 1961). Fidelity to site and mate probably strong.

AGE OF FIRST BREEDING: May return to colony in 2nd year. Of 31 recaptures of ringed birds at colony, 28 ringed as chicks 2 seasons previously and others 3-year olds. Birds 2-years old may possess adult plumage but 3-year olds may still show traces of immaturity. Breeds in 3rd or 4th year, sometimes still bearing traces of immature plumage. Thus, again like boobies, tends to breed younger than Atlantic.

NON-BREEDING YEARS: No information. Might be expected to occur.

LONGEVITY AND MORTALITY: Possible ring-loss and sporadic observation vitiates results even though many adults ringed. Adult mortality low (*c.* 3% at lowest) with almost no decrease in numbers re-observed in 3 years after ringing. Broekhuysen *et al.* (1961) figure of 12.5–15% probably too high and 5–8% probably more realistic. A 6% annual adult mortality rate would give av life-expectancy of 17.2 years. Oldest adult actually recorded just over 14 years old.

Juvenile mortality high. Only 3% of 10,145 ringed fledglings later recovered at their colonies though this is not actual survival rate. Speculatively, pre-breeding mortality *c.* 80%. Birds ringed Bird Island (1980–90) gave mean recovery rate 0.72% (highest 2.7%, 1983) (Oatley *et al.* 1992) though not possible to translate this to mortality rate. Pattern may differ from that of Atlantic gannet, with less immediate post-fledging mortality but more later. 31 2-year olds recaptured at colony had mean fledging weight of 2,937 g, slightly higher than mean for all fledglings. Most had fledged early in their season.

Atlantic Gannet *Morus [bassanus] bassanus*

PLATE 3

Pelecanus bassanus Linnaeus, 1758, Bass Rock, E Scotland.

Generic name *Morus*, now preferred to *Sula* to distinguish gannets from boobies, attributed to Viellot who in 1817 changed *Moris* conferred by Leach in 1816. Here, I use trinomial (superspecific) nomenclature (*sensu* Amadon 1966), *Morus [bassanus] bassanus*, because the 3 gannets (Atlantic, African and Australasian) not 'full' species (two last-named can interbreed) but more than 'races'.

Etymology chronicled by Cunningham (1866); Gurney (1913); see Nelson (1978a).

Other common names: north Atlantic gannet, northern gannet, soland goose. Gaelic names include Ian Ban an Sgadan' (white bird of the her-ring) and young gannet 'guga'. Pliny called them 'water eagles' and Hector Boece 'sea-herons'.

French: fou de Bassan, fou tacheté, boubic, haren-guier, marga. German: Bass tolpel, Schottengans, solendgans, seerabe (sea-raven). Spanish: alcatraz.

Description

ADULT M PRE-BREEDING: Large, dazzling white with black wing-tips. Head, nape, upper neck, according to season, deep buffish-orange to pale straw or whitish. Primaries blackish, paler on inner webs. Primary coverts and alula black; lesser primary coverts along edge of wing white or mixed white and black. Primary 10 (outermost and longest) emarginated on inner web for distal \approx 7 cm. Long, narrow wings have highest aspect-ratio of any British bird. Bill conical, moderately compressed, with 'ridge' of upper mandible broad and convex. Additional plate at angle of bill. Light blue or grey-blue, with indented black nasal grooves running along upper mandible on each side, merging into black skin on lores, the black encircling the eye and running as a line backwards and slightly downwards from angle of gape. Cutting edges of mandibles black and irregularly serrated. Tip decurved, compressed, and rather acute. Black gular strip on throat. Gape blackish; opens behind the eyes.

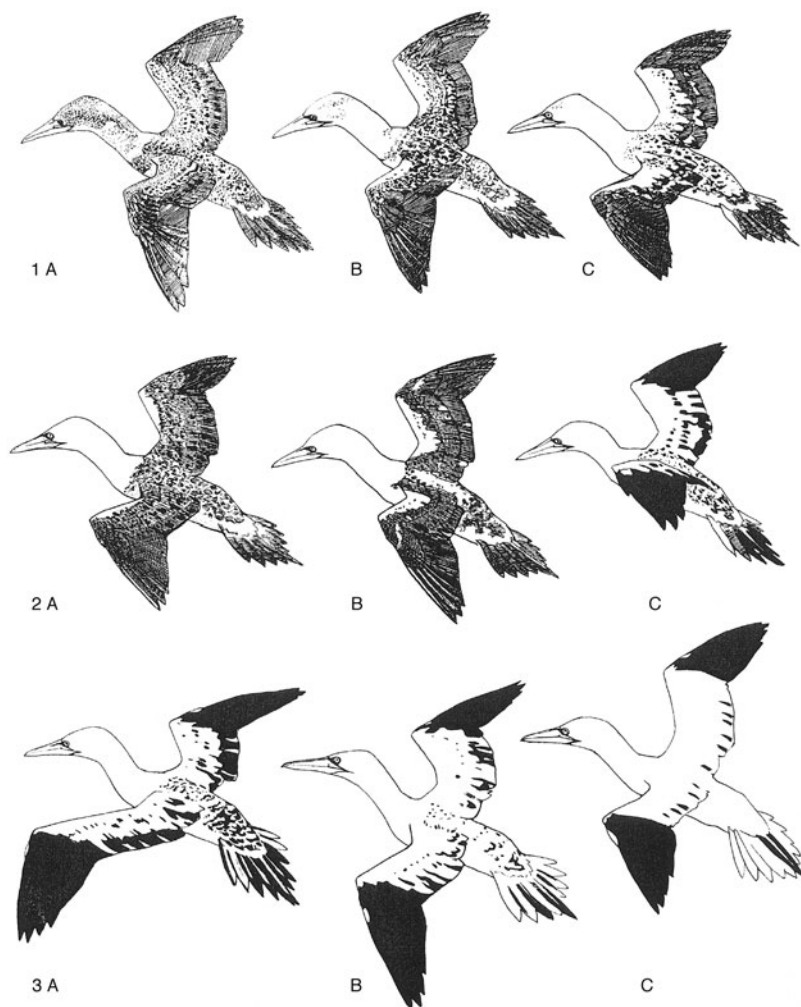
Roof of mouth ridged and oblong tongue short (\approx 6 mm). Nasal aperture linear about 3.8 cm long, with a soft longitudinal flap on each side (MacGillivray 1852). Nostrils completely closed. Ear apertures very small. Legs, feet black with conspicuous greenish lines along tops of toes converging to run up and across front of tarsi. Tarsi short, rounded in front and sharp behind. In front, three lines of small, transversely oblong scutella run down and continued on toes. First toe small and directed inwards and forwards. Third toe longest, almost equalled by fourth.

ADULT F: As male. Buff on head and neck, early in season indistinguishable from male's, later becomes pale and spotty, sometimes almost white.

A few leucistic individuals—grey or grey and white primaries. One or two albinos. A chick on Ailsa Craig with creamy down and dirty pink eyes, bill and feet (personal observation) later developed beige primaries, secondaries and wing coverts (Wanless personal communication). A male breeding on Bonaventure had 'a pink bill, orange feet and black eyes and a few black feathers in each wing-tip' (N. Gaul personal communication).

POST-NUPTIAL: Little change; paler head.

JUVENILE AND IMMATURE: Strikingly different from adult, newly feathered juvenile has grey-black upper-parts speckled with white spots, bigger and fewer on back, scapulars and wing-coverts, fine and dense on head, neck, throat. Conspicuous white 'V' on upper tail coverts with apex towards tail. Primaries and secondaries blackish-brown, bases of shafts straw-coloured and inner secondaries tipped white. Rectrices black-brown with small white tips. Paler beneath than on back. Some coal-black with few, and small, white spots, others silvery above, almost white beneath. Intermediates commoner than extremes. Bill blackish, pales with age. Feet, legs grey-black with faint lines on webs. Eye dull bluish or blackish, but may be light-coloured. Facial, gular skin and



6.30 Immature plumages of the Atlantic gannet. (From Nelson 1978b, drawings: J. P. Busby.) 1A. Typical of a bird during the latter part of the first half of its first year. The juvenile plumage in which it fledged has already abraded or been replaced on parts of the neck, producing a hint of the 'collared' appearance common in late first-year birds. Often, the wings and back are browner than at fledging. Occasionally seen in home waters in this plumage. B. Common late in the first year and often into the second. The head may remain completely dark into the second year. C. Unusually advanced plumage, occasionally found at the end of year one, probably in birds which have assumed year two plumage early. Such birds may be late year one or any stage of year two. 2A. Common early in second year; head and underparts are usually the first areas to become white. May be found late in first year. B. The 'epaulette' stage. Very common in mid-or-late-second year. Often, the white on rump encircles the darker patch, giving a 'rosette' rump. The bill may now be pale blue. C. An advanced two-year old which may retain this plumage in part of year three. 3A. Common early in third year, except rarely so much black on back and rump, through scapulars often retain black feathers. B. Perhaps the plumage most typical of mid-to fairly late-third year. C. A very common plumage in late-third and part- or all-of-the-fourth year, with black secondaries gradually disappearing to give a four-year old with only one or two and/or one or two black tail feathers(central). A few birds acquire perfect adult plumage in their fourth year.

orbital ring blackish. Middle claw and mandible serrated in adult, entire in young until post-fledging.

Underparts whiten first; forehead becomes white; broad collar spreads from upper neck onto sides of neck; white 'epaulettes' spread rapidly; back becomes boldly pied. White spreads from leading to trailing edges of wings; piano-key appearance from inter-digitation of white and black secondaries. White tail feathers spread from outer inwards until single black central tail feather and black secondary or two remain in 4th year, sometimes 5th year.

Some individuals at \approx 1 year have white on ventral surface, white collar, blotched head and beginnings of white epaulettes, others all-dark. Latter browner than newly fledged juveniles; lack white spots on back, head, neck. Often lighter area below lores and ear-coverts gives capped appearance. Variability within year class illustrated by two extremes of known 24-month-olds: least-advanced still all-brown above except for white epaulettes, head, neck and rump 'V' patch; underparts white; most advanced a few dark feathers on wing-coverts, piano-key secondaries and one or more black tail-feathers; otherwise as adult.

Field characters

See African gannet. May overlap with African in Gulf of Guinea, N as far as Biscay and possibly off Britain. An advanced 4th-year Atlantic with unusually many black secondaries and tail feathers may resemble African. Very immature birds difficult to separate, though African smaller with quicker wing-beat. In south of distribution in NW Atlantic may overlap with brown, masked and red-footed boobies (Gulf of Mexico). Adult masked has black humerals, black secondaries going right up to body and black on tail, as well as black 'face' and orange bill. Immature masked separable from immature Atlantic by former's much browner upperparts (far less boldly pied), white underparts and (juvenile) 'V'-shaped white throat, apex uppermost. Adult red-foot much smaller and slenderer.

Measurements (see Appendix)

Measurements from Funk Island (Canada), Bass Rock (Scotland) and Skarvflakken (Norway) differed

slightly in several dimensions (Birt personal communication). However, these go different ways for several morphological features; significance, if any, unclear.

Voice

Main call rasping 'arrah-arrah', varying in speed and loudness, \approx 2 calls per sec, whilst flying in to nest (not pre-landing elsewhere) and during display. When fishing or gathering nest-material communally an excited 'rah-rah' shorter, gruffer, less metallic. Soft, attenuated 'oo-ah' (hollow groan) on take-off in sky-pointing posture. In level flight may utter soft 'krok krok' like raven (German seerabe). Recognize calls of mates and probably neighbours. White and White (1970) concluded temporal pattern and amplitude only features showing consistent individual differences. Mates reacted appropriately to play-back of partner's calls (White 1971). Less evidence for young bird recognizing parents; none for neighbour-recognition. Field observations suggest both occur.

Range and status (Figures 6.33, 6.34)

CURRENT STATUS: Gurney's (1913) census gave 14 colonies. By 1935, 19 colonies and \approx 78,000 'pairs'. Gannetries additional to Gurney's: Hermaness, Noss, Saltee, Anticosti, Cape St. Mary's. Fisher and Vevers's (1943–44) survey gave 22 colonies and 165,000 + 9,500 'breeding individuals' in 1939.

In 1988 gannetries in W Atlantic (Gulf of St. Lawrence and Newfoundland) comprised 6 colonies containing \approx 42,000 'apparently occupied sites' (AOS). In 1994 (most recent) 57,308 AOS (increase since 1984 39–54%; D. Nettleship personal communication). Using amalgam of most recent counts gannetries in E Atlantic contained 303,766 AOS. Most recent figures for Iceland, 1994—Gardarsson (1995) corrects former errors, especially by (for first time) excluding non-breeders. Eastern group up from 1,550 AOS (1984) to 2,300 (1994), annual increase 4.2%; rate similar at all colonies. Two separate cliff colonies at Skrudur had begun to merge by 1994. Previous statements that Mafadrangur had been excluded from counts are mistaken. Gannets have not nested there recently. Faroes one colony \approx 2,000

6.31 World population of the Atlantic gannet.

<i>Location</i>	<i>Number of colonies</i>	<i>Number of A. O. S</i>	<i>Year of count(s)</i>	<i>Individual colonies and comments</i>
France	1	11,628	1995	Rouziec started 1939, <i>c.</i> 30 nests. Not currently limited by space and almost certainly increased since 1995
Channel Islands	2	5,950	1999	Ortac 2,500 (2,090 in 1994); Les Etacs 3,450 (3,380 in 1994)
Ireland	5	36,111	2004	Little Skellig 29,683(27,241 in 1994); Bull Rock 3,694 (1,815 in 1994); Great Saltee 2,446(2,050 in 1995); Ireland's Eye 285(188 in 2000); Clare Island 3 (new colony)
Wales	1	32,094	2004	Grassholm, at certain stages, increase due to massive immigration 30,688 in 1999.
Scotland	14	182,511	2004	Ailsa Craig 27,130(32,455 in 1994); Scar Rocks 2,394(1,952 in 1994); St. Kilda 59,622(60,428 in 1994); Flannans 2,760(1,438 in 1995); Sula Sgeir 9,225(10,440 in 1995); Sule Stack 4,618(4,889 in 1995); Fair Isle 1,875(1,340 in 2000); Foula 919(723 in 2000); Noss 8,652(7,310), Hermaness 15,633(11,993 in 2000); Troup Head 1,547(533 in 2001); Bass Rock 48,065(39,000 in 2001); Westray 14(new); Sule Skerry 57(new in 2003)
England	1	3,940	2004	Bempton (2,552 in 1999)
Iceland	8	25,437	1994	Eldey 14,100, Westmanns 9,000 Eastern Group 2,337
Faroes	1	2,340	1996	Myggenaes (Mykines Holm)
Norway	5	3,662	1995	Storebranden 1,455; Hovflesa 470, Skarvlakken 760, Innerstauren 481, Storstappen 516
Germany	1	93	2000	Helgoland 93
Canada	6	57,308	1994	Great Bird 9,229, Little Bird 639, Bonaventure 32,048, Anticosti 208, Cape St. Mary's 7,020, Baccalieu 1,041, Funk Island 7,123
Total	45	361,074		The total number of colonies listed above does not add up to 45 because some of them are grouped

Notes: 1) A.O.S: Apparently occupied sites; some counters give totals as "pair" (not to be recommended).

2) In those instances where a large colony has apparently decreased the difference is within the limits of counting error.

3) The 2004 totals are from Wanless, Murray and Harris "The status of the Northern Gannet in Britain and Ireland in 2003/04" (In Press).

4) Group of: 3 pairs, Russia, (1995).

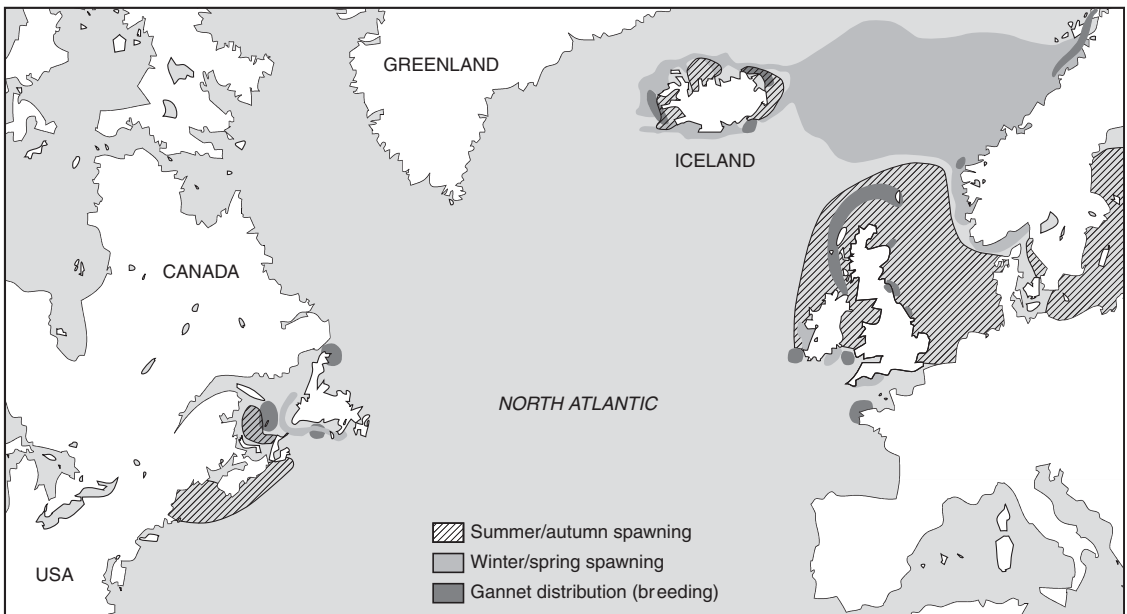
AOS in 1985. Helgoland 93 AOS, 2000. Russia tiny new group 1995. World total (Figure 6.31) 45 colonies and *c.* 361,000+ AOS at present time (at least 10% possible error).

About 85% breed in E Atlantic where Scottish population was *c.* 182,500 AOS in 2004—some 60% of world's population. Gannet colonies increasing at different rates, but overall a *c.* 3–5% per annum; a few stable or decreasing.

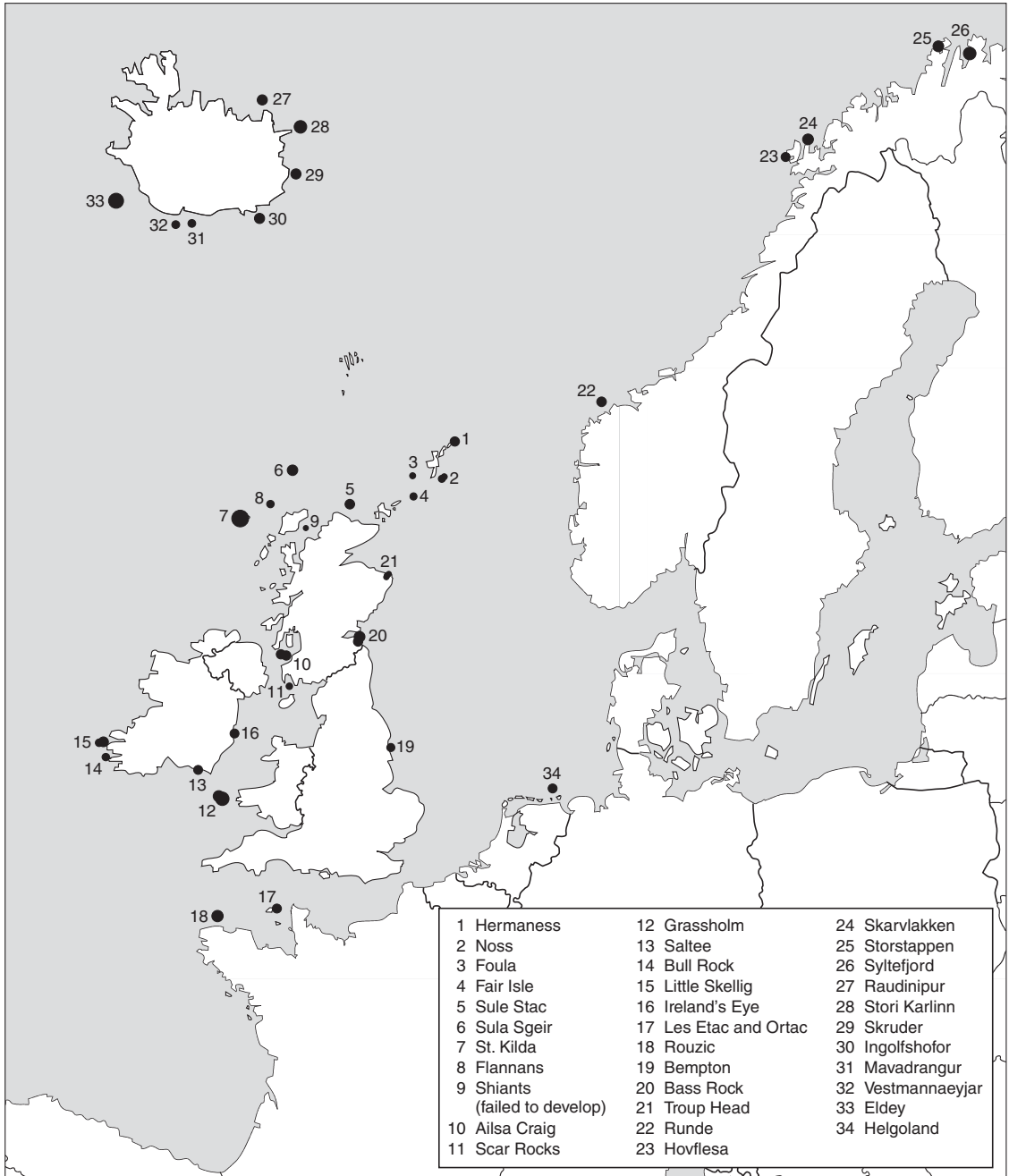
Some 60% Norwegian gannets breed north of Arctic circle, most northerly at Storstappen, 71°08' N. Most S outpost, W side of Atlantic, Cape St. Mary's (46°50' N); French colony (Rouzig) 48°53' N. Since early 1990s a few have tried to breed on moored yachts in Provence harbours. In 1996 a hand-fed chick fledged in Bandol harbour (Vidal *et al.* 1995; Zotier *et al.* 1996). In 1997, 6 were building in Sausset Les Pins, 6 in Bandol (Vidal personal communication); see also Fernandez and Bayle (1994). Probably result of general population increase with larger numbers entering Mediterranean.

Largest gannetry on single rock or island is now Bass Rock, St. Kilda (2004, 59,600 AOS)—3 separate rocks—world's largest gannetry. Historically, largest recorded gannetry was Great Bird (Gulf of St. Lawrence). With probable world population *c.* 361,000+ AOS Atlantic gannet more numerous than African or Australasian and ranks 6th in Sulidae (9 species).

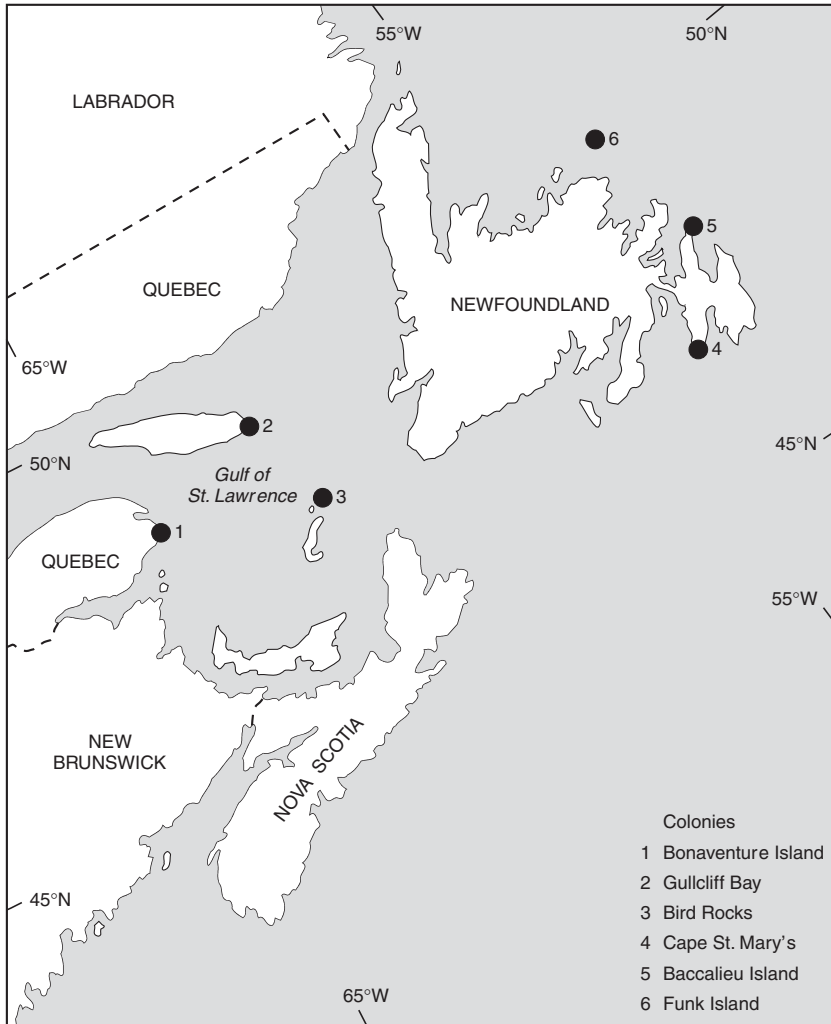
Many gannetries ancient, famous and well-documented: Salmon and Lockley (1933); Wynne-Edwards (1935a); Wynne-Edwards *et al.* (1936); Vevers and Evans (1938); Fisher and Vevers (1943–44); Dobson and Lockley (1946); Gibson (1951); Boyd (1961); Nelson (1966, 1978a, 1978b), Dixon (1971); Brun (1967, 1972, 1979); Young (1968); Nettleship (1975, 1976); Barrett (1979, 1981); Wanless (1979); Murray and Wanless (1986, 1996); Einarsson (1987); Montevecchi *et al.* (1987); Nettleship and Chapdelaine (1988); Gardarsson (1989, 1995); Lloyd *et al.* (1991); Barrett and Folkestad (1996).



6.32 Herring distribution in NW and NE Atlantic in relation to gannet colonies. (After Parrish and Saville 1965 for herring.)



6.33 Distribution of Atlantic gannet colonies in the eastern Atlantic. Postscript: Sule Skerry, Westray (Scotland) and Clare Island (Ireland), recent small colonies, have not been included in this map.



6.34 Distribution of Atlantic gannet colonies in North America. (From Nettleship 1976.)

GENERAL FEATURES, DISTRIBUTION, AND NUMBERS: Cold, rich waters over continental shelves and fishing banks. Possibly evolved from ancestral African gannets which migrated north and as adaptations to colder, stormier waters became larger and heavier and, partly for this reason, cliff-adapted. Breeding now closely linked to seasonally abundant and oily shoaling fish, particularly herring and mackerel. Energy requirements high due to costly flight (flapping), temperature regulation, exposed sites, extensive display (metabolism at nest 2.7 times

greater than predicted for existence-metabolism of non-passerine at 10°C (Birt-Friesen *et al.* 1989). Reinsch (1969) linked gannet distribution to herring whilst Brun (1972) postulated similar links between Norwegian colonies and herring and capelin. Link between mackerel and breeding gannets (Nelson 1978a, 1978b). All St. Lawrence colonies lie near rich fisheries and Bird Rocks gannetry in area fed by currents from zones of high primary productivity, rich in spawning fish. Prey fluctuates from year to year. Wide food spectrum and extensive and exclusive

offshore feeding niche are important adaptations. Can forage far afield and exploit stocks unavailable to terns, puffins, kittiwakes, etc.

Northerly limits of herring extend well N of gannet's present limit, 71°08' N in Norway. But at herring's northernmost limit Arctic summer too short for gannet's 26–30 week breeding period. This excludes many islands off Greenland, Spitzbergen, Novaya Zemlya and Franz Josef Land. Herring's SW limits about latitude of entrance to Biscay and gannet may not penetrate in large numbers much further S than Brittany.

Dissected and island-strewn W seaboard of Scotland, Wales, and Ireland supports most of world's population. Offshore waters N and W of Scotland focal point, embracing Iceland, St. Kilda complex, Faroes, Shetland, and colonies in W of Scotland S to Scar Rocks. Within this area lie the few ancient colonies that are static or increasing slowly. Except for the Bass, E coast of Britain largely lacks suitably high and cliff-girt islands. High mainland cliffs around Troup Head now colonized and St. Abb's Head may soon be. Troup and Bempton (England) probably founded by Bass birds.

W seaboard of Europe little favoured until establishment of Rouzic, Brittany (Siorat and Rocamora (1995) give population changes 1939–94) and Norwegian colonies. Norway lacked gannetries in modern times, though some existed at least 7,000 years ago (Montevecchi and Hufthammer 1990). Norwegian colonies, prospected in 1946, grew by immigration from Bass and St. Kilda and probably from further N. Five colonies, holding *c.* 3,700 AOS grew at mean overall rate of 13.9% per annum, far above intrinsic recruitment. Recently 2 Norwegian colonies declined as others increased, perhaps related to fluctuations of fish stocks (Barrett and Folkestad 1996).

Continental shelf off E Canada, where polar and warmer waters mix, highly productive. More than half W population of North Atlantic breeds on Bonaventure Island (Gulf of St. Lawrence). Gannets of Newfoundland and Gulf of St. Lawrence (*c.* 10.4% of world population) probably largely isolated from those in eastern North Atlantic. In 1972–73 *c.* 32,700 pairs, 70% in the 3 Gulf of St. Lawrence colonies and 30% in the 3 Newfoundland colonies. Census in

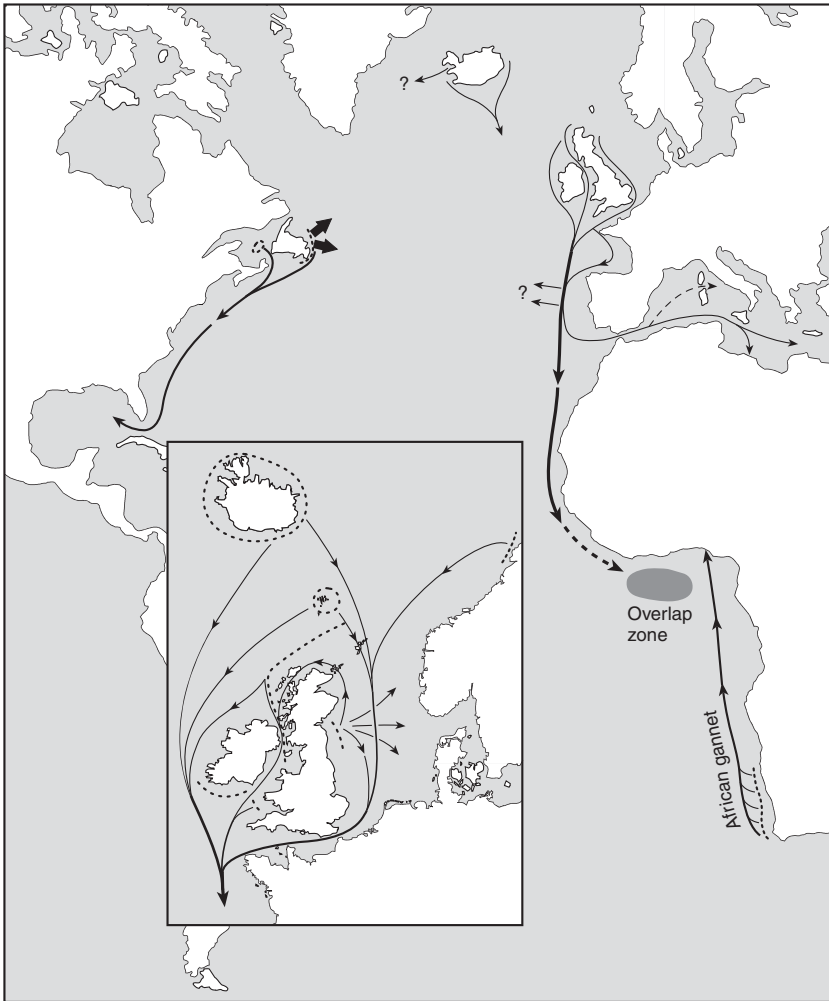
1984 indicated *c.* 40,000 pairs (27,800 Gulf, 12,300 Newfoundland), increase of 22% over 1972–73, followed by further 13% increase (1984–88). 1994 survey gave 57,308. Pesticide pollution slowed increase. Colonies on Bonaventure and Anticosti Island had decreased since 1969, possibly due to pesticides, whereas Newfoundland population had not. Av per annum increase in W Atlantic similar to E, but some colonies, especially Bonaventure, increased massively, others not at all.

20th-century increase attributable to less persecution and perhaps latterly to increase in fish discards. Specacular recent increase reflects population expanding from increasing base. Present world population of *c.* 45 colonies (depends on definition) (Figure 6.31) and *c.* 361,000 AOS has risen from 22 colonies and 83,000 AOS in 1939 (converting 165,000 \pm 9,500 individuals of Fisher and Vevers into AOS without hypothetical corrections). Individual colonies vary greatly in rates of increase, both in particular years and over longer periods, due to variable rates of immigration. But overall increase approximates to known recruitment and mortality (Nelson 1978a).

Substantial source of error at some large gannetries, for example Bass and Grassholm, lies in several thousands present *but not holding definitive sites*. Counts which purport to be 'nesting pairs', 'breeding pairs', 'pairs' or 'apparently occupied sites' should (but usually do not) exclude these. Proportion of non-site-holding birds differs between colonies, in different parts of same colony and at different points in season. Nevertheless, gannet census figures notably complete.

COLONY INTERCHANGE: Colonies receive incomers, sometimes from far afield. Some have increased more than 10 times as rapidly as potential intrinsic output. Large, growing colonies such as Grassholm in 1970s and 1980s may receive thousands of immigrants in one year. Large gannetries attract streams of prospectors which may establish breeding sites. Isolated ones may attract fewer immigrants. Until recently Bass, only gannetry on Britain's E coast, probably grew by its own output.

Young birds from Little Skellig (full?) probably re-established Grassholm; birds from Ailsa Craig



6.35 General features of the southward migration of juvenile Atlantic gannets. Inset: main routes from breeding areas in east Atlantic.

probably established Scar Rocks and Bass birds Bempton and Troup Head. But adults, having once bred, do not then breed elsewhere. Well-established gannetry rarely shows substantial year-on-year decreases.

MOVEMENTS: Seminal early paper on gannet movements in eastern North Atlantic by Thomson (1974). Juveniles migrate $\approx 5,000$ km S, almost to equator. Post-breeding adults migrate or disperse. Encountered mainly over continental shelf waters often within 800–1,600 km of breeding places, sometimes much further. Birds in 2nd-year to

sub-adult plumage remain variable but decreasing distance S of breeding latitudes, or may visit colonies during breeding season. Then move S again but less far. Immatures and possibly mature-plumaged pre-breeders may wander between colonies. Adult-plumaged birds may be seen, in breeding season, hundreds of km from nearest gannetry. Extensive foraging movements in some months overlap with migration and dispersion. Both adult and immature gannets may be seen over much of range at any time.

Autumn movements often associated with calms between depressions and clearing frontal conditions. Migrating gannets often fly low, sometimes



6.36 Recoveries, during their first year, of Bass Rock juveniles. 154 recovered July–October, 3 recovered November–June. (From Nelson 1978b.)

back-tracking, singly or in loose groups. Do not form distinctive chevrons typical of fish-laden birds returning to colony. Walker (personal communication) noted ascent in thermals off Cape St. Vincent and these birds may then have moved off at height.

Averse to land, but may cross from Forth to Clyde (Scotland). Many (Bass?) juveniles, Sep/Oct, inner Forth; subsequent movements not known.

No indication of colony-specific wintering areas but birds from Ailsa and Grassholm may arrive Biscay earlier than Bass birds (more immediate exit to main migratory route). Multidirectional nature of dispersion-migration (see below) not surprising if it derives from sulid dispersal. Some Bass juveniles move N before migrating S—perhaps a relic of northward movement of ancestral African gannet from which



6.37 Recoveries during their fourth year or later of Bass Rock juveniles. (From Nelson 1978b.)

Atlantic may have evolved. Main southward route of gannets on E side of Atlantic is in Figures 6.35, 6.36 and 6.37. Southerly autumnal passage off Cape Clear (SW Ireland) heaviest on record, peaking at 4,000 per hr. Some reach Gulf of Guinea and overlap with African gannets. Thousands penetrate Mediterranean (see below) and (rarely) Adriatic off Croatia. Relatively uncommon in Baltic, especially in winter; most recoveries in approaches, although Bass bird, in

June of its 5th year, recovered Lithuania 55°N 23°E. Recoveries (mostly summer) N of most northerly British colony include birds born on Grassholm and Skellig. Probably extensive foraging or reconnoitring trips.

First birds to disperse, August onwards, slightly before migration of juveniles, are 2nd and 3rd-year; non-breeders. Then flood of juveniles, other immatures and later adult post-breeders. Adults

predominate on passage for a period then migration slackens in Dec–Jan when home waters are quiet though some adults return to colony in Jan. Further S, considerable movements, N and S. North Sea numbers lowest in Feb (*c.* 60,000) 97% adults and mainly in W half (Tasker *et al.* 1985). In May, twice this number, mainly in centre and off E Scotland, when 10% immature. Numbers in Nov even higher but fewer immatures.

Clear of Ushant, passage to Biscay and beyond on wide front. First youngsters reach S Biscay before end Aug. Off NW Spain, even in early Sep, bulk of southward passage is of juveniles. By early Oct passage spectacular; by then about a third are adults. Passage peaks soon after dawn though it may continue all day and increase again in evening. Over a day (Oct) hourly rates (Cape St. Vincent) *c.* 500–800. By Nov southward passage (*c.* 800 per hour) 88% adult. Dec passage *c.* 700 per hour (Walker personal communication). Birds rounding Cape very vocal, uttering tri-syllabic ‘grank-grank-grank’ calls (function not understood).

In January 1994 and 1995, 98% and 97% of birds moving N off Cape St. Vincent, also large numbers off Cape Clear, were adult-plumaged. At Butt of Lewis gannets pass in thousands Jan–Apr. Immatures flood through in May and June when numbers build up at breeding colonies.

MEDITERRANEAN PASSAGE: Passage via Straits of Gibraltar. Earliest juveniles arrive end Aug, moving on to Algeria late Sep by which time juveniles have peaked at Gibraltar. Adult and immature birds (2nd–4th year) enter Malaga Bay mainly in second half Oct (Paterson 1987). In 1987 hundreds of transects between Algeciras and N Africa produced 5,567 sightings of which 2,797 were juveniles or 1st-year birds and 1,599 adults (Hashmi 1993), most moving E but *c.* 20% W. Migration of juveniles peaked 30 Sep and continued until mid-Nov. In this period *c.* 43% Mediterranean juveniles returned to Atlantic, eastward migration alternating with westward. Adults move in by late Sep and peak a month later. Smaller proportion return to Atlantic. Hashmi calculated that Sep–Dec 1987 between 16,600 and 19,400 gannets entered Mediterranean without soon returning, and total

wintering population *c.* 20,000–25,000 birds—a significant proportion of eastern North Atlantic population. Age-groups Sep 1980–Dec 1983: juvenile–1st-year 980 (57.4%), 2nd-year 172 (10.1%), 3rd and 4th-year 53 (3.1%), adult 501 (29.4%). Many birds remain into 2nd year. During winter birds range at least as far as Sicily; a few as far as Cyprus, Egypt, and Israel. Return to Atlantic occurs late Jan–Mar, at which latter time movement of adults greatest (Paterson 1987). Finlayson and Cortes (1984) estimated spring passage through Strait of Gibraltar *c.* 7,500 birds; 80% adults. At Cape St. Vincent Walker recorded northward passage of 432–676 per hr, Jan–Mar 1996; 83–95% adult. A few birds summer in Mediterranean.

Duration of immature bird’s sojourn in S waters highly variable. A few, less than a year old, and good numbers of 2nd-year birds, present in ‘clubs’ at gannetries but at that age most are still south of Ushant. As they mature, fewer and fewer remain or over-winter S of Biscay and some early 2nd-year birds probably over-winter in N waters.

Walker noted westerly movement out of Gulf of Cadiz, hinting at possible transatlantic passage. 60 years ago Wynne-Edwards (1935a) noted gannets are sufficiently pelagic to allow movement between Europe and Canada and cited records from Greenland and Northern Labrador. Yet the two populations almost entirely distinct.

Migrating gannets feed opportunistically, then raft (*c.* 2,000 off Cape St. Vincent personal observation). Feeding and weather-induced movements confuse picture. For example, at Cape St. Vincent, even Oct–Dec, gannets of all ages move north and south (Walker personal communication).

MOVEMENTS OF CANADIAN GANNETS: Canadian juveniles migrate to SW for some 4,000–5,300 km taking them to *c.* 26°N, mainly (juveniles and immatures) Gulf of Mexico (Moisan and Scherrer 1973). This counterpart of gannet migration in eastern North Atlantic similarly moves birds from food-rich but cold and turbulent winter waters to calmer, warmer though less productive areas. Breeding later than in E Atlantic and migration, which starts late Sep, quickly peaks mid-Oct; less scope for lingering in rapidly deteriorating

conditions, or for overwintering in home waters. Birds reach Florida by Dec and Gulf of Mexico by Jan. 40% of recoveries of juveniles are from Gulf of Mexico compared with 13% of older immatures and 8% of adults. As in E Atlantic initial direction taken by some birds (SE) differs from main one. Vagrant to Cuba (Wallace and Fillman 1994).

Immatures leave wintering areas in Mar and arrive at Bonaventure in May. By Jun, 1st-year birds spread out from Gaspe to Gulf of St. Lawrence. When they arrive in breeding area conditions are relatively mild and fish plentiful. Return journey estimated at up to 90 km a day; 3 times as rapid as southward migration.

RINGING RECOVERIES (BRITISH TRUST FOR ORNITHOLOGY): Since Gurney first marked Bass gannets in 1904, 57,855, mostly chicks, have been ringed up to and including 1993, and 3,413 recovered. Recovery rate rose from 3.2% up to 1937, to 5.4% up to 1968, 5.65% to 1973 and 5.9% to 1993. Considerably higher than for Canadian population or for African or Australasian gannet, probably because coastlines bordering North Sea form particularly favourable catchment area off densely populated W seaboard of Europe. Ringing recoveries from most northerly gannetries (Norway) do not differ substantially from pattern elsewhere. No colony-specific anomalies in routes or destinations, though information mainly from Bass.

ATTAINMENT OF FLIGHT BY MIGRATING JUVENILES: Fledgling begins migration by swimming. Flightless period speculatively 3–7 days. Reports that juveniles may take-off immediately after fledging and fly around own colony probably mistaken; some British juveniles on wing early enough to visit non-natal colonies. An Ailsa-ringed juvenile visited Grassholm *c.* 2 weeks after fledging and occasionally a bird-of-the-year may be seen Aug-Sep flying around or even landing in a gannetry.

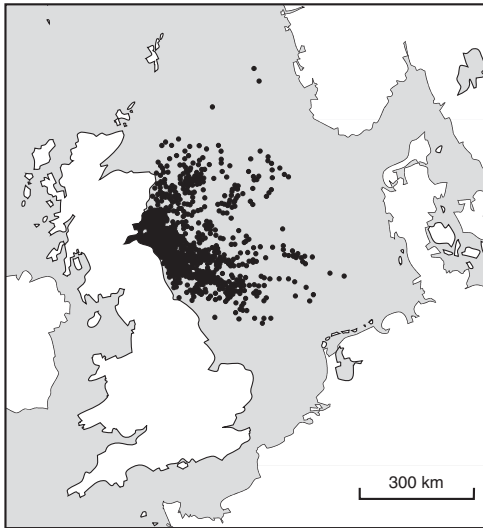
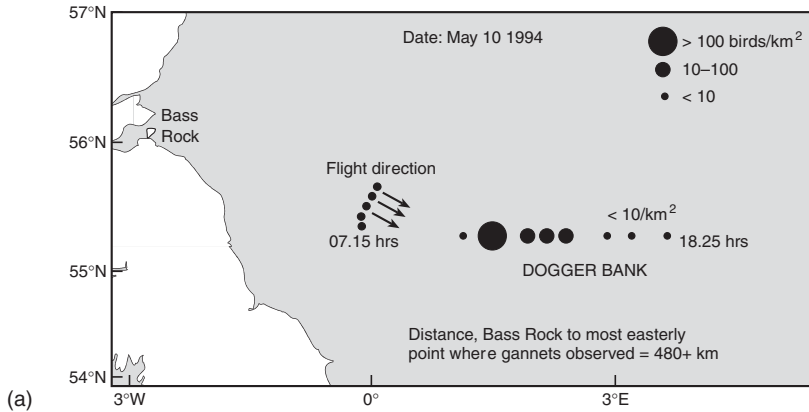
Pace of migration variable. An Ailsa bird reached Morocco in 11 days but 1st-year birds may linger at some points S, for weeks or months. Probably few E Atlantic birds reach S limit by 2 months after

fledging. Most move quickly into W European waters, then S from Nov onwards.

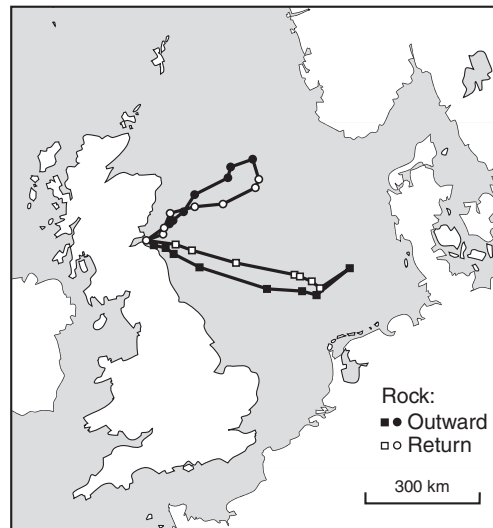
Foraging and food

Marine, offshore. Breeding gannets may forage at least 320 km from colony. Ringed birds, probably breeding, recovered up to 640 km from colony. Tasker *et al.* (1985) conclude foraging trips rarely >150 km. Garthe *et al.* (1999) using logger-equipped birds, showed that they spent 39–49% of their time in the colony, 22–30% flying, 22–34% swimming. Trips av 13 hr (2 hr 45 min–27 hr 08 min) with estimated max range 128 km. Bass gannets favour specific feeding areas (e.g. Farne Islands and 'Wee Bankie'). Camphuysen *et al.* (1995b) showed that perhaps 2% Bass gannets head purposefully for a predictable feeding area (Dogger Bank, North Sea) at least 280–320 km away. They forage far out in North Sea; some reach Norway (see Figure 6.38b) (satellite telemetry—Hamer *et al.* 2000). Mean duration of foraging trips positively correlated with colony size; indicating gannets from larger colonies have to travel further to find food (Lewis *et al.* 2001). Tendency to feed on shoaling fish, and visual attraction of diving gannets, encourages feeding in predictably productive area, even far from colony. But also fish opportunistically, occasionally close to colony. On W of Scotland, feeding areas of several colonies may overlap. Aerial surveys in Labrador, April–Oct, showed low densities in offshore and inshore waters, (av) 0.02 and 0.04 birds per km² respectively (Kirkham *et al.* 1985). However, highly communal fishing the rule. Aggregations off W Scotland may be >1,000. Camphuysen *et al.* (1995b) recorded mass-feeding of gannets in association with dolphins at Dogger Bank. Gannets not only fed with dolphins which forced fish to surface layers, but followed them (similarly, boobies follow tuna).

Gannets moving purposefully fly low over surface with semi-continuous wing-beats 170–90/min, gliding, banking, rising and falling. In presence of shoal they beat upwind with downward-pointing bill, often circling. May rotate on descent, to enter water steeply, obliquely, or backwards of vertical. Wings shoot backwards, tips beyond tail; perfect arrow-head. Lee and Reddish (1981, film analysis)



(b) Each dot is a recorded position of a tagged gannet; 1,327 locations from 17 chick rearing adults over 45 days



(c) Typical foraging routes from Bass

6.38 (a) An example of the foraging range of the Atlantic gannet, (After Camphuysen *et al.* 1995b.). (b) and (c) Foraging ranges of Bass gannets. (From Hamer *et al.* 2000.)

calculated that point at which gannets streamline becomes earlier as height of dive increases . . . 'the greater the risk of injury and the larger the margin allowed for that error'. Schoener (1994) uses the gannet's dive to theorize about visual information and its incorporation into physical action. In feeding-frenzy gannets plunge at random and strike or pursue fish underwater. At other times track fish by sight. May power down but usually plunge by grav-

ity *c.* 100kph when hits water, often with massive impact. Penetrate only few metres by dive alone, further by swimming. No reliable information about max depths; gannets caught in nets difficult to interpret. Most submergences 5–7 sec, many up to 10 sec and a few up to 20 sec. Emerge usually into wind, often in different direction to entry. May immediately rise and dive again from 3–4 m in arc. Usually swallows fish underwater but may disable large ones

on surface; may swallow tail first. If successful shuffles wings (bathing movements), false-drinks and head-shakes. If rises immediately probably been unsuccessful.

Gannets cleave water with closed bill and take fish on rising or open mandibles when impetus slackened. Rarely, they pierce the fish (fate of puffin seen draped round gannet's head). Popular story of enticing gannets to dive onto herrings nailed to plank. Several accounts of gannets diving onto decks or into trawler holds, and one of gannets diving into fish-curing shed in Penzance (Nelson 1978a).

Congregate over shoal with raucous gabbling. Communal fishing may enhance individual success

without being cooperative. Yet likely that gannets coordinate diving; immediately before concerted dive, vocalizes with loud and rapid 'grank' call. May pass and re-pass over conspicuous shoal of mackerel without diving.

Satiated gannets rest on sea, near feeding group. Homing skeins usually tens or scores. Observers far at sea record thousands leaving feeding area and heading directly for a gannetry (Camphuysen *et al.* 1995b).

Wind-ruffled sea may assist fishing, perhaps obscuring prey's vision and slowing reaction time, but winds of Beaufort Force 8 or more inhibit fishing or even flying. Gannet's weight enables it to fish in winds which would incommode light birds. African gannets (lighter than Atlantics) often stop if winds exceed Force 4. Gannets will fish in dusk but do not land in colony after dark. Will dive around floodlit fishing vessels. Will scoop up fry, fish on foot in shallow bays, presumably for sand-eels, dive from surface and pursue fish with half-opened wings like guillemot. E.T. Booth's captive gannets dived like a coot.

Significant scavengers behind fishing vessels (see Camphuysen *et al.* 1995a), although of 15 scavenging species only 3.7% were gannets (still many thousands). During experimental discarding in May, gannets took 5 times more round fish than other scavengers. Dominated skuas, greater black-backed gulls and fulmars (see Garth and Hueppop 1998). Immatures disproportionately common. Nevertheless, fishing vessels largely ignored whilst gannets travel directly to definitive area far out in North Sea.

Many scavengers fall to net, hook, or gun. Become conditioned to noise of diesel engines and lifting gear and respond before fish seen. Record of gannet joining gulls behind tractor! Piracy rare.

Breeding strategy depends on predictable availability of nutritious fish, but wide prey spectrum buffers against shortage. In Newfoundland main foods, decreasing order of importance: mackerel, capelin, squid and some years Atlantic saury, herring, and cod (Montevecchi and Porter 1980). Food fish fluctuate in abundance—partly natural, partly man-induced. Nakashima (1996) reviews capelin biology and shows, since 1991, changes in spawning behaviour, age classes and distribution



6.39 Diving in the Atlantic gannet. (From Nelson 1978a, drawing: J. P. Busby.)

(Canada) and links this to changes in Aug diet of gannets. Montevecchi and Myers (1997) discuss importance of annual variability brought about by oceanographic influences on timing of inshore movements, sizes, abundance and reproductive condition of gannet prey species in NW Atlantic. In Britain mackerel, herring and sand-eel important; in Norway saithe and herring (Montevecchi and Barrett 1987). Herring comprised 69% of energy value of sampled food loads even though herring less abundant than saithe around Norwegian colonies. Parental food-loads in Norway contained less energy than in Newfoundland and Scotland but food varies from year to year. In Newfoundland, when gannets caught many fewer than usual of a dominant prey-species, local pelagic fisheries likewise failed (Montevecchi *et al.* 1988). Likely that overfishing by man affects gannet diet. Kirkham *et al.* (1985) found marked differences in species-composition of Funk Island gannet regurgitates during different parts of season.

Overall, mackerel main prey, particularly in late July–early Aug, when chicks impose high demands. Mackerel fishery failed August 1981 and gannets switched to herring and capelin. Squid significant in some areas; in NW Atlantic *Ilex illecebrosus* formed 10% by mass (Montevecchi *et al.* 1988) but not reported in Norwegian diets. Median weight of food swallowed (logger equipped bird) 101 g ($n = 32$); max 745 g (Garthe *et al.* 1999).

Seem to catch sufficient food with ease. Only pelecyaniform to guard chick continuously throughout development and pair attend 15% of daylight hours (Bass) even at peak demand. Burden of extra (donated) chick did not appreciably curtail chick-guarding, pair-attendance, or chick's fledging weight (Nelson 1964) yet chick grows more rapidly than any other sulid and lays down large fat reserves.

In winter gannets fare well, and are fat on return to colony early in year. In summer, *contra* many seabirds, never show evidence of food shortage.



6.40 Gannets scavenging trawler waste. (Photo: R. Reinsch.)

Habitat and general biology

(See Fig. at end of ch. 5, Nelson 1965, 1978b)

HABITAT: Marine, offshore and pelagic. Weight, which permits deep-plunging and handling of large, muscular prey (masked booby similar size but *c.* 50% weight) and long, narrow wings, which facilitate far-foraging, impose requirements for breeding. Wind important for landing, departure and aerial reconnoitring; islands, with slopes and cliffs thus favoured; excludes mammalian predators. Mainland cliffs disadvantaged by foodless hinterland. Prefers precipitous cliffs with ledges large enough for substantial nest, but can use narrow or sloping ledges and flat tops of islands which may contain 'lanes' used by departing birds. Nests from just above splash zone. Rapidly expanding areas attract disproportionately more recruits.



6.41 Cliff and slope habitat favoured by Atlantic gannet.

Cliff adaptations (Nelson 1967a) include use of excreta to cement nests; failure to roll displaced egg back into nest; restrained begging of young (avoids falling); failure to discriminate against strange young; clinging ability of chick; chick habitually faces inwards; black plumage of juvenile may inhibit attack by male.

COLONIES: Highly traditional, over centuries. Notable for large size, high density and regular spacing of nests at *c.* 2.3 per m². Expand by creeping outwards whilst maintaining approx standard density. Consistent and high-density social rather than topographical phenomenon.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually. Occupies colonies several weeks before egg-laying and after chick's departure; loses foraging time but safeguards site. Arrive suddenly at colony, often in large numbers flying in steady procession, Dec to early Feb. No obvious N-S divide; Icelandic, Norwegian, and Noss birds arrive Jan–Feb whilst on Rouzic (Brittany) massive landings 3rd week Jan (Siorat personal communication). Experienced males first to arrive (Bass). Within large colonies arrivals locally dense; suggestive for groupings within colonies and sub-group synchrony but difficult questions. In Canada return late March–early April when colonies mainly free of snow and ice.

Early return facilitates early laying with suggestion of higher post-fledging survival (Nelson unpublished—based on ringing recoveries). Gannetries tend to empty precipitately Sept–mid-Nov (weather dependent) some weeks after most young fledged. No gannetry continuously occupied throughout a year, even by roosting birds (*contra* boobies).

Egg-laying seasonal but protracted. 1st and median egg dates highly consistent for individual gannetry, and marked synchrony, but considerable spread. Bass gannets lay mid-March (earliest record 2 March highly exceptional, giving July fledging) to early July. Most eggs laid April, early May; mean and median egg *c.* 20 April ± 4 days. Has been so for at least 130 years. On Ailsa median egg *c.* 10–14 days later. On Rouzic (Brittany) mean laying date (1988–94) 9–24 April but in all years except 1988



6.42 Atlantic gannets spreading up the NW slope of the Bass Rock.



6.43 Continuing spread of the Bass Rock gannet.

between 9 and 12 April (Siorat personal communication). Late chicks (replacement layings) may linger until mid-Nov (Bass).

Date of laying affected by: age-experience of female; length of tenure of site and mate; size of colony. Position effects (centre-edge) not independently important; edge birds tend to be younger and less experienced. Over several years, *but not necessarily in any one*, distribution of laying dates probably optimal for survival of young (including post-fledging). Considerable spread mitigates unpredictable disasters e.g. sleet and rain with high winds in July can kill downy young too large to be brooded. If *all* young were at this stage, year's output could be jeopardized. Similarly, onshore gales 'gannet winds' can cast newly fledged young ashore in 'wrecks'; spread reduces this effect.

Timing of breeding season utilizes favourable feeding conditions in pre-laying phase and growth of chicks. Around Iceland, saithe and herring abundant in winter and gannets visit breeding stations in Jan, lay March and peak April. Bass gannets exploit sand-eels early in year. Abundant early food facilitates deposition of fat at this demanding time. Canadian colonies *c.* 1 month behind British and end sooner. On Bonaventure 1st egg last week April or first of May and last egg by third week June. Spread about two-thirds that of Bass. Much of late start made up; peaks only 2–3 weeks behind Bass—71% of total eggs laid by 15 May and 95% by 30 May, 1967 (Poulin 1968). Modal laying point mere 5 days after onset and by 2nd or 3rd week May nearly as many birds had laid as on Bass. Gonads may

mature more rapidly on Bonaventure following mass return and thus high-level social stimulation.

Plentiful food during chick-growth permits rapid development and large fat deposits. Early fledging avoids equinoctial gales. Fat deposits fuel migration and support juvenile until it acquires hunting skills.

In addition to approximate timing and synchrony attributable to changes in temperature and daylength and to circannual rhythm, *individual female* affected by social factors and age-experience. Exposure to behavioural stimuli advances laying-date and enhances sub-group synchrony. Also, laying date advances with age for 2–3 years after first breeding. Bereavement and consequent re-mating retards laying date (Nelson 1978b: 118–26). Pairs in which old male partnered new female produced eggs about 10 days later than mean for group, and pairs in which new male partnered new female laid 18 days later than mean. Thus age-experience of male affects laying date of female, mechanism not known.

Lifetime frequency may be unusually high for long-lived seabird; few, if any, 'rest-years' except enforced by loss of egg, chick or mate. On Bass, of 252 pair-years (e.g. 5 pairs each remaining together for 5 years equals 25 pair-years) there were 251 breeding attempts. Only one pair, for one year, apparently did not attempt to breed (Nelson 1978b: Table 22).

TERRITORIAL BEHAVIOUR: Most of adult life spent at nest-site. Social (mainly territorial) activity within colony uniquely intense and seasonally prolonged.



6.44 Overt fighting can be fierce and prolonged, injuries are exacerbated by the attacks of surrounding birds.

After 2 or more years' attendance at a 'club' males reconnoitre from air or ground before establishing a site; may involve fierce fighting. Site-owning females accept intruding males but violently resist females. Overt fighting (Figure 6.44) rare in established birds but ritualized threat frequent and follows same seasonal pattern and intensity as other aggressive behaviour.

Bowing (Figure 6.46), gannet's ritualized site-ownership display elicited by intrusion or social disturbance, evolved from post-landing behaviour (ground biting). Females share site-defence, but bow at lower intensity than males.

PAIR INTERACTIONS: Male's advertising (female-attracting) display is inconspicuous (Figure 6.47); may be modified version of territorial display. Approach of isomorphic female elicits aggression but defused by ritual appeasement (turning bill

away). As acceptance proceeds, 'mutual fencing' (greeting ceremony) intensifies.

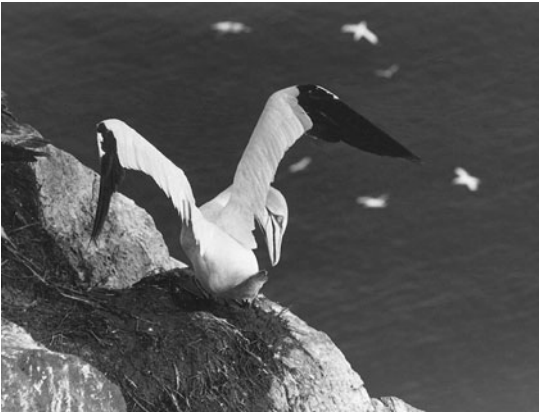
After initial acceptance male repeatedly departs, circles colony, returns and nape-bites and pair greet'. These rituals preface first prolonged absence and condition female to remain on site.

Pair-bond reinforced by prolonged greeting (Figure 6.48) following each reunion and site-threatening event. Greeting resembles territorial bowing performed by partners facing each other in contact; followed by intensive mutual preening.

Skypointing (Figure 6.49) Common to both sexes, often prolonged; precedes movement, usually from site. Bird pivots with busked wings and drooping webs. Neck lengthened, pointing bill vertically, which displays black gular stripe. Sepulchral groan 'oo-ah'. By signalling departure skypointing inhibits partner from leaving; thus site constantly guarded against plunder.



6.45 Severe damage may result from fighting.

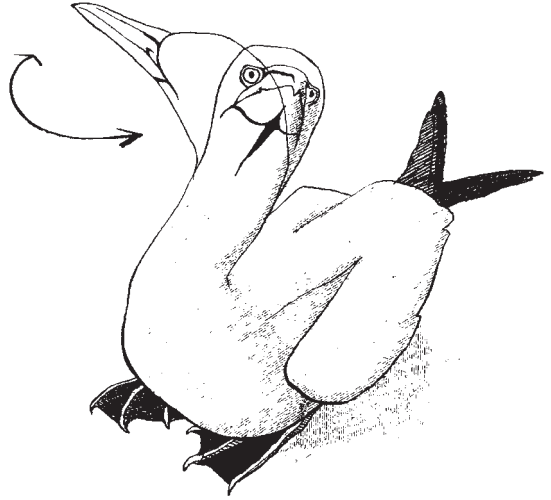


6.46 Bowing; the ritualised site ownership display.

Skypointing homologue in boobies (see fig at end of Chap 5) functions as sexual advertising. 'Pre-departure' original signal; behavioural 'emancipation' has occurred in boobies, whilst gannets retain original context and function (details Nelson 1978b).

COPULATION: (GFA)

NEST: On cliff ledge, steep, slope, or flat, bare rock or soil. Jan–Oct; males gather material (mainly grass) from windward slopes, communally but unaggressively; rapid calls as in communal fishing. Trips from nest-site (up to 11 per hr) prefaced by sky-pointing, followed by greeting ceremony and often copulation and mutual nest-building. Seaweed gathered from surface after shallow landing dive. Debris (plastic, synthetic net, line) pose severe threat. May catch

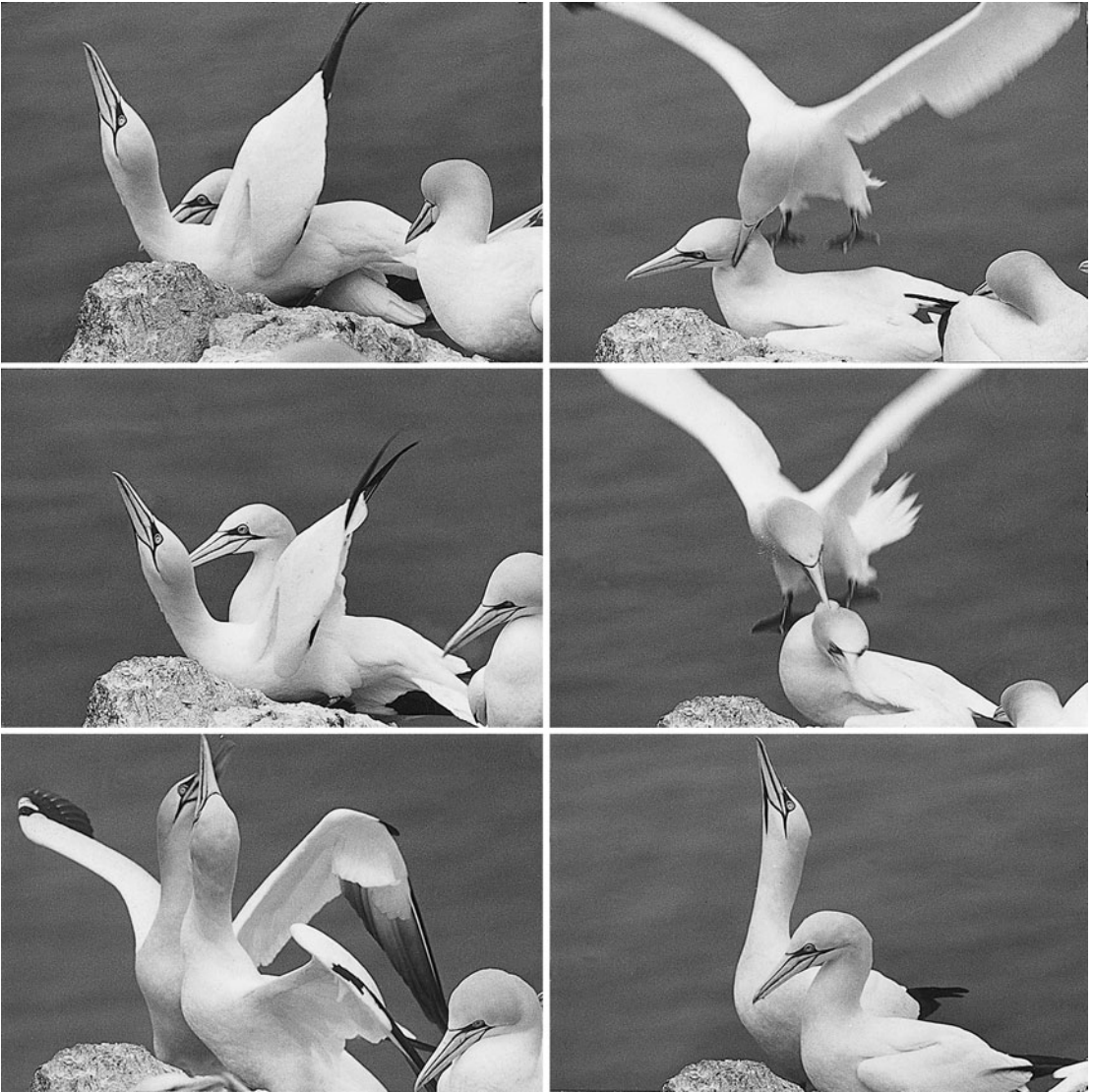


6.47 The inconspicuous, male sexual 'advertising' display in the Atlantic gannet. Non-homologous with its functional equivalent in the boobies. (From Nelson 1978b, drawing: J.P. Busby.)



6.48 Two year-olds (non-site holders) practising ritualised greeting behaviour (mutual fencing).

in angle of gape, bind mandibles or anchor adult or chick. Half nests in colony may be contaminated. Material positioned with rhythmical, small-amplitude, side-to-side movements of head and tremoring of mandibles. No ability to suit material to site; may persist with grass instead of seaweed on steeply sloping ledges. As adaptation to cliff-nesting, deposits thick and sticky excreta onto side of nest. With mucous from seaweed and regurgitate (fish slime,



6.49 The male's successive (ritualised) departures (with skypointing) and returns (with nape-biting) and the greeting ceremony (mutual fencing), reinforce the pair bond.

bones) forms pedestal capable of holding 10,000 g. Raises adult and egg or chick above ooze which collects in wet weather. Cup, lined with fine grass and feathers, formed by applying webs and lower breast and turning. Body moult after egg-laying provides feathers. During incubation tucks moulted body feathers around flanks, conserving warmth. Captive gannets plucked their own feathers (Booth 1887). Removes hard seaweed vesicles or stones thus preventing point-pressure damage to egg.

Gannets on slopes and tops of vegetated islands remove vegetation and top-soil, leading to erosion and exposure of bare rock.

EGG/CLUTCH: 78.06 (62.5–87.5) × 49.1 (43.1–53.7) n = 100 Scotland; 77.6 × 47.0 n = 44, 82.27 × 49.66 n = 20 Canada. Weight: 104.5 (81–130) n = 393 fresh Bass Rock; 98.1 (70–118) n = 57 some part-incubated Bonaventure. Calculated Bonaventure fresh weight 103.29. According to Montevecchi and

Porter (1980) Cape St. Mary eggs 114.1 ± 1.7 , which seems anomalous. Shell weight: 11.59 (10.8–12.9) $n = 100$; 11% of fresh weight, unusually high. Percentage of yolk (15.5%), fat content of yolk and albumen (25.8%) and energy content (0.897 Kcal.g⁻¹) are lowest recorded for any avian egg (Ricklefs and Montevicchi 1979). At 3.3% of female's weight Atlantic gannet's egg is lighter than those of African and Australasian gannets (3.9%); hatchlings of two latter face possible longer period without food (longer foraging).

Early eggs heavier than later, probably because mainly from older females. Clutch invariably one. Two eggs rare; produced by 2 females (triangular relationships) or rolled in.

Given extra egg reared twins with surprising ease (Nelson 1964, 1978a). At several stages, including heaviest, some individual twins outweighed av singleton of same age. Twins fledged at 94 (84–103) days against 90 (84–97) for singletons. Slightly longer fledging period of twins unlikely to be critical. Parents of twins produced 76% more young than parents of singletons. Since more than 70% of normal singletons die before breeding, mortality of twins would have to be unrealistically high to contribute fewer breeding recruits. Normal variation in singleton fledging weight far greater than difference between twins and singletons. With only 4 days' difference in fledging dates between twins and singletons, chances 50:50 that they encounter favourable weather. Thus twins gave significant reproductive advantage.

REPLACEMENT LAYING: Eggs lost within *c.* 25 days replaced in 6–32 days (usually 19–21, Bass) unless lost late in season. Few females re-laid a second time. Instances of 3rd and 4th re-lays (Poulin 1968). Replacement interval up to 39 days (mean 14 days). 17% re-laid in 5 or fewer days and by 30 days 96.2% had re-laid. After 43 days no replacement.

INCUBATION: Days prior to egg-laying, female sits in nest centre and begins foot movements associated with incubation. Actual laying takes about 2 minutes. Tail depressed at last instant and appears to guide egg into cup. Eggs laid at any time of day or during night. May tuck it on top of webs before putting webs on top of egg—an incubation method

noted by Conrad Gesner in the 16th century. Webs cover *c.* 63 cm², considerably more than upper surface of egg. Mostly, egg incubated lengthwise, along bird's head–tail axis. Frequently shifts position and re-tucks egg. In hot weather may transfer it to upper surface or shade it. Can hatch two eggs though takes *c.* 2 days longer; 2-egg clutches increase re-settling and egg-tucking with consequent slight cooling. Females breeding first time are as efficient as experienced birds but lose more eggs (may ignore or dislodge newly laid egg). Precise parallel in chick care. Female may accept donated egg without having laid that season, though if she has already ovulated, likely to reject it.

Lacks adequate retrieval below nest rim but can roll egg into cup from rim. Never incubates egg outside nest, nor builds new nest around it. If male present when egg laid, female may soon vacate it. From time of male's arrival to female vacating egg av 8 min whereas reverse 3 min. Most arrivals dawn to midday with second major influx early evening. No change-overs during darkness. Relieved male may bring nest-material before departing.

Incubation period Bass 43.6 days $n = 83$, 75 accurate to within 24 hours, 8 to within 6 hours. Distribution: 42 days (9 cases), 43 (25), 44 (38), 45 (9) and 46 (2). Infertile eggs incubated for up to 102 days. Mean period on Bonaventure 43.9 days despite lower ambient temperature, indicating efficiency of beneath-web incubation.

Incubation shifts on Bass, (1962) first half incubation period, male 37.2 (7–84), female 30.8 (4–70). Second half, male 33.2 (6–62), female 29.1 (10–46). Shortly before hatching shifts decrease sharply.

CHICK: Hatchling *c.* 70–80 g, *c.* 11 cm long. Loose, blackish skin. Eyes dark bluish; partly or entirely closed until day 2 or 3. Bill dark, paler towards tip; whitish egg-tooth. Legs, feet deep grey. Sparsely covered with first-generation white down with hair-like tips. Replaced by fluffy down; long and dense on sides and underparts, short and sparse on forehead, around eyes and on throat. Second-generation down shed as juvenile feathers grow but not replaced by them, nor replaced directly, in continuous growth, by under-down of feathered stage, though this succeeds it (Witherby *et al.* 1940). Week 1: by end sparse white down and blackish skin very



6.50 Gannet chick (embryo) shortly before hatching. Yolk-sac attached, egg tooth prominent. (From predated egg)



6.51 Six week-old chick with parents.



6.52 Young gannet with 'wig' ('Parliament goose') aged 9-10 weeks.

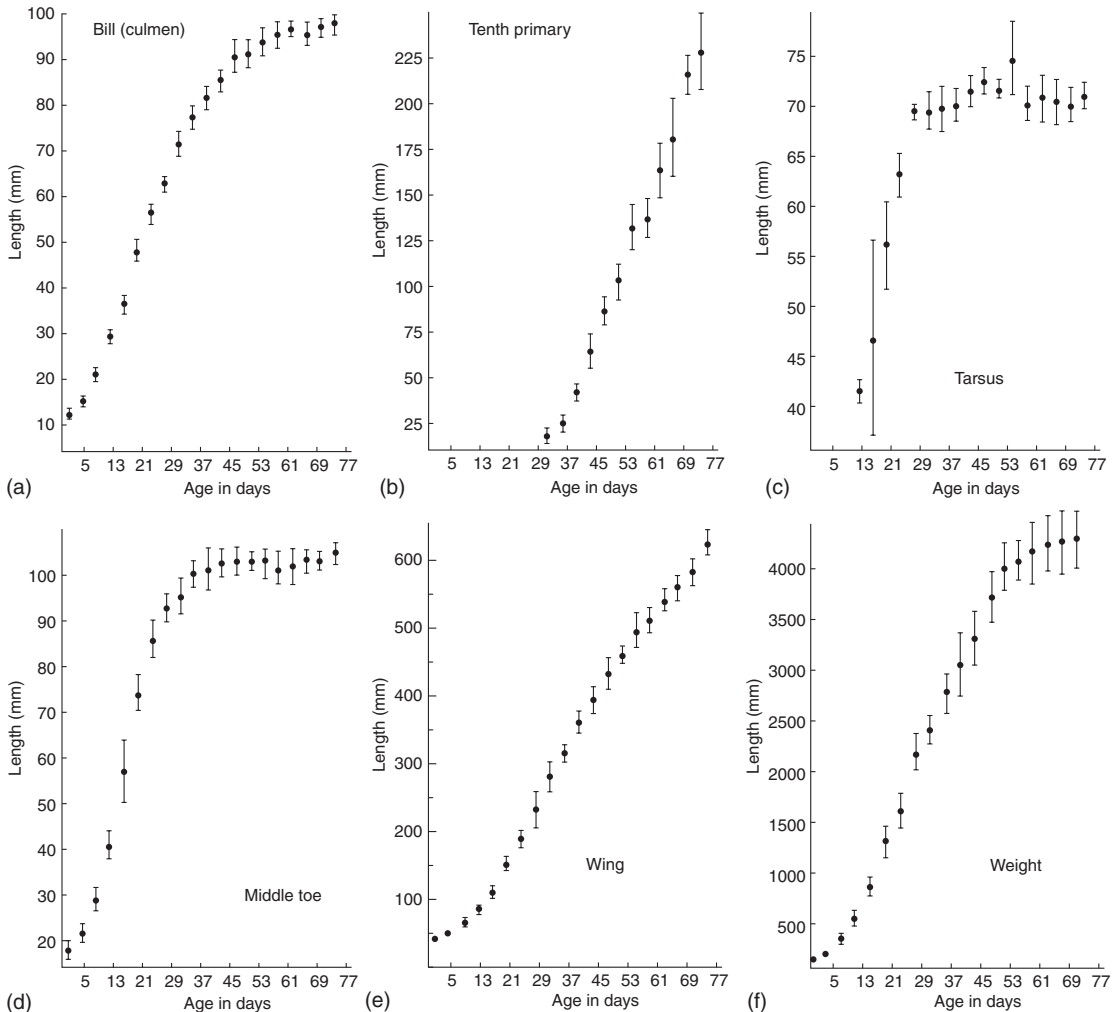
evident. Week 2: down thickens and by end chick larger than adult's webs. Head and neck bareish, radio-ulna and 'hand-wing' still blackish. Down scrubby. Week 3: down lengthens, fluffy, wings

well-clothed; bill black and shiny. Becoming too big to be fully covered. Week 4: large and fat (c.1,800 g), down long and fluffy. Wing and tail-feathers not yet erupted. Week 5: primaries and rectrices may show

black through down. Approaching adult body-size. Week 6: scapulars, wing, tail-feathers conspicuously black though still largely down-covered. Week 7: black on wings, back and tail steadily expanding. Chick still covered with long, white down beneath, and on head and neck. Back shows down-with-feathers. Week 8: advanced chicks beginning to lose down from feathered forehead, back and tail. Week 9: down thinning beneath though still thick on flanks, belly, and parts of neck, where resembles wig ('parliament goose'). Week 10: down clears but some remains on nape, flanks, and back. Chick now

mainly black. Week 11: early in week 11 most advanced chicks retain wisps on nape and flank; by end may be completely clear. Retarded chicks may not reach this stage until 93 days.

Growth (see Figure 6.53). Mean max weight of $\approx 4,100$ g between 65 and 75 days and although mean fledging weight $\approx 3,900$ g some chicks considerably less. Weight may drop substantially from earlier maximum—e.g. from 3,600 g at 72 days to 2,700 g at 79 days, recovering to 2,900 g at 87 days. Mean weight of 26 juveniles (Ailsa Craig) that fell short of sea 3,659 g (3,000–4,320) (Wanless 1979).



6.53 The growth of different parts shows different patterns. (From Poulin 1968.)

Large deposit of sub-cutaneous and perivisceral fat supports juvenile when learning to fish.

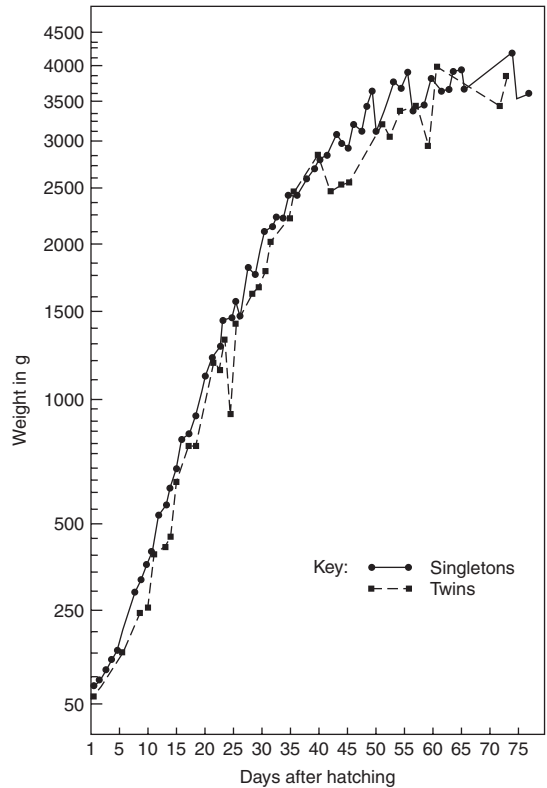
Growth of bill, wing, foot and longest primary show different patterns (Figure 6.53). Most reliable parameters for estimating age are bill and total wing-length. Bill (culmen) grows fastest days 9–33: after day 49 difference between consecutive (4-day interval) mean measurements no longer significant. Curve flattens at culmen length of 96 mm (adult's c.100). Little variation around mean culmen length for any age; bill important in extracting food from adult and shortness would handicap.

Days 1–77 wing grows steadily; each (4-day) mean point differs significantly from preceding and following one. No difference between years. *Reliable attainment of optimal pre-fledging wing-length largely independent of fluctuations in food.* Longest primary (10th) appears day c. 29 and grows at 5.5 mm per day during period of most rapid growth. By fledging time wing, c. 450 mm, still short of adult length (501–35), deficit may be made good before juvenile can sustain flight.

Middle toe grows rapidly from 18 mm (day 1) to 97 mm (day 33) during which period reliable indicator of age. Rapid growth in first month, almost to adult size, means that when chick too large to be brooded, its webs are adequate for losing body-heat. Considerable variation in growth of tarsi emphasizes significance of consistent web growth (important in swimming phase of migration).

At physiological level, percentage of water in body decreases linearly with age, from c. 85% at hatching to 70% at 50 days (Ricklefs *et al.* 1985).

CARE OF YOUNG: Chipping egg transferred to top of webs which prevents collapse of shell. Transference stimulated by chick's vocalization but depends on maturation of appropriate response; some birds breeding for first time continue to incubate underfoot and crush chick. Vince (personal communication) detected movement of chick in artificially incubated eggs 13 days pre-hatch. Started breathing from air-space 2.5 days before hatching; began to cheep 8 hours later. Pipping to hatching 43 hours. Some females prise eggshell off hatching chick. Shell may be left in nest, placed on rim, flung away, dropped over side



6.54 Growth of twins (artificially produced) compared with singletons. Despite the huge biomass reared, there is no significant difference in growth. (From Nelson 1964.)

or trampled. Incubation stints shorten prior to hatching; mostly female takes final one. Hatchling brooded on top of webs but even experienced birds sometimes tread on it. Most losses around hatching and in first c. 5 days. May be due to inadequate chick-feeding mostly by inexperienced adult. Difficult to determine to what extent adult stimulates chick to feed. Parent offers food in various postures without obvious stimulation from chick (however, vocalization from hatching egg may trigger regurgitation). Head may be turned upside down so that chick feeds from trough of upper mandible (cf. pelicans). First feed may be given before chick clear of shell.

In experimentally twinned nests hatchlings, though requirement negligible, fell behind singletons in weight, suggesting adults programmed to feed one chick without begging. If so, pre-set

quota would be split two ways. Alternatively (or in addition) adult might respond to movements of chick; if not precisely proportional to chick's hunger, twins would not provide twice-feeding stimulus of singletons. Later, when chicks beg persistently and in well-oriented way, they elicit twice normal amount of food and growth keeps up with that of singletons (Figure 6.54). Adults respond to 'yip-yip' begging call and pestering by regurgitating food into throat, never into nest. Spilt food re-swallowed or flung. No record of bringing water.

Body care limited to preening young and brooding it until c. 3 weeks old, but not thereafter sheltered from sun or rain. Large chick has to endure this. Prolonged wetting and chill can kill downy chick and severe weather can cause considerable mortality. Wide spread of laying mitigates this.

BEHAVIOUR OF YOUNG: At 2 days chick gular flutters and pants; cannot thermoregulate until c. 3 weeks (thicker down, enhanced ability to generate

body heat by muscular activity, Montevecchi and Vaughan 1989). Until 6 weeks may sprawl, head on ground. When feathered, stands or sits with head in scapulars; occasionally still lie prone, which adults never do. Cannot seek shade; loses heat by panting, gular-fluttering and exposing excreta-wetted webs to air for evaporative cooling.

Gape-distension occurs 1st day. After 1 week begins to flap wings and rotate head and neck. In 2nd week stretches wings sideways and arches them with head and neck horizontal and tongue-bone depressed. Prolonged wing-exercising regular after flight feathers erupt and is unfailingly stimulated by rain when colony sprouts myriads of black wings (no adults). When exercising wings, usually faces wind but on narrow ledges faces inwards. Although exercise excludes walking or jumping many fall—main cause of mortality at this stage. Perfunctory self-preening begins c. 2 weeks. From c. 10 weeks chicks may preen parents, reciprocally or unilaterally, but whereas adults focus on head



6.55 Feeding by incomplete regurgitation, after restrained begging (anti-falling).

and neck, chicks preen anywhere. Once feathers well grown (c. 8 weeks) chicks oil them from preen gland like adult.

Small chicks do not produce faecal sacs and cannot void clear of nest, which becomes fouled, although adults continue to fling spilt fish away.

From c. 2 weeks may place nest material on rim and make building movements. Non-ritualized threat against other chicks from c. 4 weeks, ritualized threat by time fully feathered. Trespassing chicks attacked with high-pitched 'yapping'. From c. 7 weeks some chicks (males?) frequently threaten and attack parents, eliciting appeasement from female and retaliation from male. Attacks uncoordinated; violent but erratic jabs, excited yapping, contortions, self-biting (cf. pelicans) and perfunctory preening. This apparently dysgenic behaviour presumably concomitant of ontogeny of aggression. Appeasement behaviour appears during first month. Chick lies flat, bill tucked beneath body presenting arched nape to attacker. Thick layer of muscles enables chick to survive prolonged attack. Stimulus for bill-tucking is tactile—gentle tapping will elicit it. From c. 9 weeks chicks face away in adult-female manner, sometimes reverting to infantile bill-hiding. Adult 'pelican-posture' rare in chicks but commoner in feathered juveniles. Ill-defined site-ownership display (bowing) sometimes from large young. Fully grown (male?) may show incipient version of greeting display (mutual fencing) with female parent. By time it fledges chick may have shown all adult behaviour except copulation, nest-digging, sky-pointing and behaviour associated with incubation and chick care. Strikingly, even when it departs on first 'flight', never sky-points before movement (though lengthens neck). Sky-pointing develops only in social context of pre-breeding 'clubs'.

Chicks learn surroundings; when large enough can regain nest from several metres without prior exploration. Can climb into nest from 3–4 weeks. Toes flexible and sharp-clawed; beak acts as lever, not for grasping. Too unbalanced to move downhill. On flatish ground ability to recognize nest-site from new perspectives enables it to regain site if fledging attempt aborted. May enable pre-breeder to recognize area of birth. Cliff sites and

aggressive neighbours deter wandering, and chicks remain on or near nest until they fledge. Adult on-site does not discriminate between own and strange young even of different size, but attacks any chick approaching from *beyond* nest. Chicks respond to voice of parent, but displaced chicks readily accept strange adults, thus accounting for some records of twins.

Adults, even non-breeders, and immatures on fringe, conspicuously aggressive to unattended young; breeding birds may leave own nest to attack even small, downy chicks. Even dead chick, downy or feathered, lying outside nest may release prolonged attack. That an unguarded chick sitting quietly on its nest may incite potentially lethal attack despite prolonged appeasement must exert strong selection pressure favouring chick guarding, hence gannet's unremitting attendance (*contra* boobies). Attacking non-trespassing chicks seems dysgenic extension of otherwise functional behaviour. Apparently of no advantage to performer, it has persisted because selection pressure cannot eliminate it without disproportionate penalty. When few adults remain, late chicks wander and 'play'.

Black plumage of juvenile seems disadvantageous in plunge-diver because against light sky makes them more conspicuous to fish at critical time of unaided transition to independence. On nest black plumage of juvenile may inhibit attack from male parent, by presenting visual stimulus opposite to that of adult, whose size and posture it resembles. An attack could fatally dislodge it. If black plumage eliminates this, its survival value may outweigh disadvantages. After fledging, ventral surface quickly pales (hunting camouflage); dorsal surface remains black.

FLEDGING: 1–4 days before fledging, takes up sleeked, long-necked, forward-leaning posture, peering down, oblivious to all else. After many minutes may turn away from sea and relax. May alternate between these two states 30–40 times in a day. If about to jump, swallows convulsively (inflating air-sacs) and half-lifts wings, jerkily. Often patters feet and head-shakes. Takes-off after 2–3 preparatory wing-flicks. Cliff birds immediately airborne but wind and updraught may destabilize



6.56 Adult with juvenile ready for fledging. Maximum plumage contrast between adult and juvenile may reduce the danger of the adult attacking and displacing it.



6.57 Fledging is precipitate and irrevocable. Under difficult wind conditions some crash with fatal injury.

followed by crash-landing which, unless into sea, can be fatal. Achieves stable flight with shallow wing-beats and can cover several kilometres. On flat ground juveniles flounder through dense ranks of aggressive adults. If forced to lie doggo may become fouled, attacked and die. But some, *en route* to edge, may be accepted, preened and even fed, and occasionally two appear on one nest.

Contrary to many accounts, pre-fledging gannet is not starved; may be fed in hour it fledges; but becomes less prone to beg so it, not adult, controls food intake.

On sea juvenile bathes, wing-flaps, and begins swimming. May be attacked by many adults for long

period but this common only early in season. No reliable record of normally fat youngster managing to take off from sea in hours following descent though most try. May be 2–3 days before able to take off (no firm evidence) and at this point vulnerable to ‘wrecks’ due to onshore winds. Adults remain at colony and play no part in juvenile’s post-fledging life. Records of old and young together at sea are juveniles attaching to passing adult.

Fledging period 90 days (84–97) $n=111$ Bass Rock; commonest 89 (17%). Chicks from cliff-edge and inland nests fledged at 88.9 days ($n=36$), so ease of departure made no difference. Chicks of first-time breeders and of experienced parents fledged at 90.1 ($n=70$), showing gannets achieve fully competent foraging and chick-feeding before attempting to breed. Twinned chicks fledged at 94 days (89–103) $n=24$. Chicks fledging in Aug 87.8 (83–90) $n=11$ and Oct 86.4 (85–88) $n=7$ took significantly less time than Sep fledgings (1–15 Sep: 91.5 (86–97) $n=42$; 16–30 Sep: 90.0 (83–96) $n=39$). Probably means that early chicks grew fastest and late ones fledged prematurely due to general desertion of colony and fewer feeds.

Bonaventure birds fledged 90.6 (82–99). 75% of Bonaventure young fledged 2–20 Sep peaking 16–20 Sep, little more than week behind Bass despite later spring return. Chicks from replacement eggs took 87.4 days $n=12$ probably due to rapidly deteriorating weather in late Sep. Late young not underweight.

POST-FLEDGING: All 3 gannets unique amongst *sulids* in lacking post-fledging feeding. Atlantic gannet’s seasonally abundant food facilitates rapid growth, early fledging, and substantial reserves of fat. Clearly adaptive in such a dense nesting and aggressive species, since return of fledgling for feeding would be impracticable. Also impracticable to accompany (and feed) juvenile to sea. Interwoven nature of breeding strategem and associated adaptations evident.

BREEDING SUCCESS: Hatched from laid: 82% ($n=495$ 1961–63, 7.3% apparently infertile, 11% lost, reason unknown); never below 85% (1964–76, less intensive observation, Bass). Little or no egg-loss to predators. Freak weather can cause

egg-loss on cliff-sites; updraughts can sweep birds off nests. Exceptionally low nests may be washed out. Only 38% success Bonaventure (most lost eggs but 16.5% failed after normal incubation period; chilling—disturbance—and toxic chemicals possibly responsible, Poulin 1968). In 1967, with severe snow, Bonaventure nests protected by trees hatched more than unprotected groups. On Bass, inexperienced birds hatched 62.5% compared with 86% by birds breeding for at least 3rd time. Difference due to egg-loss and ineffective incubation.

Fledged from hatched: 92.3% ($n=500$, 1961–63: 89%, 94% and 94%) Bass; 93% (1974), 91% (1975) (Ailsa Craig, Wanless 1979); 78.3% (over 2 years, Bonaventure. Disturbance led to loss of small chicks).

On Bass chick-loss due to: weather (high winds, low temperature and prolonged rain), dislodgement by departing adult (not parent); inadequate care of hatchling by parent and disturbance by man. In 1974 Wanless found 468 fallen chicks at base of Ailsa cliffs: less than 2 weeks (8), 2–4 (58), 4–6 (58), 6–8 (62), 8–10 (45) and 10+ (237). Montevecchi and Wells (1984a), Cape St. Mary, witnessed 236 departures—205 successful. Successful fledgings significantly higher from ocean-facing cliffs (93%) than from plateau (70%) or slopes (77%). Not clear that all apparently 'unsuccessful' fledgings were so but figures suggest advantage of cliff-sites.

Fledged from laid: 85% April eggs, 67% May eggs ($n=145$, Bass 1961); 91% April eggs, 90% May, 75% June eggs ($n=159$, Bass 1962); *c.* 73% (*c.* 1,800 nests, 8 years, less complete Bass records, excluding replacements); 80% (mainland colony, Bempton, Charlton personal communication); 53% (Troup Head, Scottish mainland, reason unclear but probably difficulty of counting, collating various observations and perhaps vulnerability to foxes, Wanless *et al.* 1996); 70% or more (Ailsa); *c.* 80% (Grassholm); 85.7%; 86.7%; 90.9%, 85.4%; access strictly controlled and disturbance minimal (Rouzic, 1991–94, Siorat); 46.5 + 2.3% 1970–74, with 62% highest figure (Skarvlakken, Norway; severe weather coupled with disturbance probably responsible, Brun 1974); 29.6% 1966 and 67,

31.4% 1970, 44.7% 1974 but then rose to more normal levels, 68.6% 1976, 77.3% 1979, 75.1% (1984 Bonaventure). Increased success coincided with marked decline in DDE, DDD, PCBs and dieldrin residues in eggs. Previously, DDE highest ever recorded at any gannetry worldwide (whole-egg levels up to 100 ppm). These toxics had reduced hatching success (Chapdelaine *et al.* 1987). Success of replacement eggs only 37% Bass, 7.5% Bonaventure.

Small and growing gannetries lower success, partly due to higher proportion of inexperienced breeders. Within large gannetry different sub-groups differ in breeding success due to different composition, topography and aspect. No evidence that fringe sites less productive than central if allowed for age and experience. Fringes have higher proportion of young pairs and more disturbance. Gannetries < *c.* 50 pairs seem less successful than large ones. As Bempton grew, success became equal to that of Bass, a good comparison since Bempton, offshoot of Bass, situated on E coast, shares some of same fishing grounds and is inaccessible to disturbance. As threshold between small and 'sizeable' is crossed, breeding success improves and rate of increase of colony rises (Nelson 1978b: Figure 55). Presumably both are social effects; frequency and intensity of display higher in large masses than in semi-isolated groups (Nelson 1965).

FIDELITY TO COLONY, SITE, AND MATE: Having once bred, gannets return to that colony.

Natal philopatry strong but impossible to quantify due to difficulty in detecting all returners and unknown extent of emigration. On Bass, colour-coded young tended to return to part of rock in which born; only 3 exceptions out of 150 sightings. But emigration and pioneering also important. Even Bass produces some emigrants, although until recently it was only gannetry on E Britain. Bass-ringed chick found breeding in Norway, and the two British E-coast colonies (Bempton and Troupe Head) at least partly from Bass recruits. Conversely, Bass receives immigrants, although probably few. An Icelandic and an Ailsa bird have been recovered there. Situation on W seaboard of

Britain very different—e.g. Grassholm and Ailsa, receive many immigrants. Number of their emigrants impossible to judge.

Many thousands, mainly immatures, visit non-natal colonies. 'Peer attraction' probably one factor. In rapidly increasing gannetry, pair-formation facilitated by local concentrations of advertising males and prospecting females. Disproportionately large numbers may be attracted into particular gannetries at certain times.

Natal philopatry inevitably lower in gannetries such as Little Skellig and Sule Stack which have little or no spare space.

Males return to site of previous year. Where both partners remained alive 94% males, 88% females faithful to site-mate. Females slightly weaker attachment to site reflects fact that, if bereaved, she may respond to advertising male on another site, though in 10 of 13 instances bereaved female acquired a new mate on her old site. Of 16 bereaved males 15 acquired a new female on same site and 16th moved next door. Fringe-site males do not attempt to move into centre.

In large gannetry, some nests occupied but not bred on; reason unknown. These are in addition to 'club' birds and pre-breeding fringe areas.

AGE OF FIRST BREEDING: Males acquire definitive site during 4th or 5th year, though rapidly expanding groups contain many 3–5 year-olds. A high proportion breed in year following site-establishment.

Both sexes can breed successfully in 4th year (4th birthday in June and thus early in 5th year when actually rearing a chick). Such birds can lay after spending only small part of previous season in attendance. But many 3 and 4 year-olds remain outside breeding population. Elsewhere (Cape St. Mary), shooting of adult-plumaged gannets attending a nest, but with no contents, has shown they were physiologically immature (Davies and Keynes 1948). Unknown whether gannetries contain mature birds (plumage and gonads), but below e.g. nutritional threshold.

In known-age pairs where partners of different age, males were year older than mates in 6 cases but

none other way round. Where one partner more-immature plumage than other, it was female in 49% of cases and male in 19%; in remainder ($n = 153$) sexes looked equally mature. In 5 cases in which partners known to be 4 years old and compared on same day, female looked more immature than male.

In sexed 3 year-olds, 10 females but only 3 males had several, or many, black secondaries and tail feathers and 3 of the females but only 1 male still showed black scapulars. Of 43 known 4 year-olds, 4 females but only 1 male had 2 or more black secondaries and 11 males but only 1 female had adult plumage.

Thus females breed when younger than males and take longer to attain adult plumage. Later breeding of males could reflect high energetic cost of site-establishment. Male's mature plumage (when same age as immature-plumaged female) confers 'badge' of maturity when defending site (if merely by presence).

Extent of deferred breeding may be partly determined by social factors such as need for protracted site-attendance and thus ability to locate food expeditiously, which requires local knowledge. If first 2 years spent S of home waters and further year or two acquiring fishing lore rather than physical skills, observed pre-breeding period is explicable.

NON-BREEDING YEARS: Non-breeding, adult-plumaged gannets at a colony are: bereaved or recently divorced, with or without a new partner; newly established birds in 5th year or older; failed breeders; adults with topographically difficult sites or (speculatively) below some 'fitness' threshold. Possibly (but no evidence) may be resting between breeding years. Many non-breeders exist at colonies where plenty of topographically suitable sites.

LONGEVITY AND MORTALITY: Annual adult mortality probably around 5% implying an adult life-expectancy of more than 20 years (oldest ringed bird 30 years). Pre-breeding mortality notoriously difficult to ascertain. Assuming life expectancy of 20 years from 3rd year onwards and annual breeding success of 75%, each pair rears av 15 chicks. If population stable, only 2 would be required; 86%

would die. But gannets increasing *c.* 3% per annum. On these assumptions, total pre-breeding mortality *c.* 77%; most in 1st year. Thomson (1974) showed that of 1,600 recoveries related to age, 54.2% fell in 1st year. Thereafter, correcting for recoveries already taken into account: year 2, 34.8%; year 3, 34.6%; year 4, 33.5%, year 5 33.1%.

These are not actual mortality rates but only recovery rates according to age.

Most recoveries are in Oct and largely of juveniles which die, mainly through starvation, during transition to independence. Recoveries on W side of Atlantic (Moisan and Scherrer 1973) add little to above. See GFA for causes of death.

Abbott's Booby *Papasula abbotti*

PLATE 4

Sula abbotti Ridgway, 1893, Assumption Island.

French: fou d'Abbott. German: Abbott-töpel. Spanish: piquero de Abbott.

Sub-species

None extant but *Papasula abbotti costelloi* (Steadman *et al.* 1988), extinct sub-species (Marquesas); differs in size and some osteological characters.

Olson and Warheit (1988), based on my skeletal material from Christmas Island, give Abbott's booby generic status within Sulidae; lacks derived characters shared by *Morus* and *Sula* and forms separate, primitive clade. Above authors give 5 characters separating Abbott's from other sulids; in particular character of vertebrae and a unique feature which appears to distinguish Abbott's from *all* other birds: sclera of eye-balls including ring of sclerotic ossicles, entirely ossified to form hollow sphere; significance unknown.

Description

ADULT M PRE-BREEDING: Large. Head, neck, underparts snow white; wings, scapulars deep blackish ageing to deep burnt brown with variably buff-edged coverts. Partly white covert feathers may show on wings. Carpal joint spotted white extending onto leading edge; conspicuous in flight. Inner webs of black primaries with broad white segment (except on distal fifth) spreading over entire inner web, then both webs towards base. Secondaries white inner webs and bases. Back boldly patterned; variable black blotches on white. Tail feathers black with irregular white tips. Upper tail coverts mainly white, some



6.58 Abbott's booby. The dark eye is exceptionally large, bill coarsely toothed and (unusually for a sulid) black-tipped.

with black centres. Axillaries and underwing white except for tips of primaries and extreme tips of few inner secondaries. Conspicuous black thigh patch posterior to vertical line of leg, extending to undertail coverts. Feathers here have triangular dark areas on one side of shaft. Large, deep bill conspicuously serrated, with flattened keel towards tip of lower mandible. Bill noticeably hooked with, near tip, slight gap between opposed cutting edges. Livid blue-grey, faintly tinged pink, with final quarter conspicuously black. Gular skin lead grey with delicate greenish line separating from throat. Skin around eye bluish-black, orbital ring blackish, dark brown iris, all giving appearance of huge, dark eye. Legs, feet deep grey with distal third of web black. Tarsal scutes particularly robust. Not conspicuously short-legged (*contra* arboreal red-footed booby).

ADULT F: As M but larger with conspicuously rose-pink bill.

POST-NUPTIAL: No obvious change.

JUVENILE AND IMMATURE: uniquely like adult M, even to colour of bill, until pink tinge indicates female. Slightly more obvious buff edges to scapulars and wing-coverts not diagnostic at distance or compared with faded adult. In hand, bill slightly greyer than adult's, but with same black tip.

Field characters

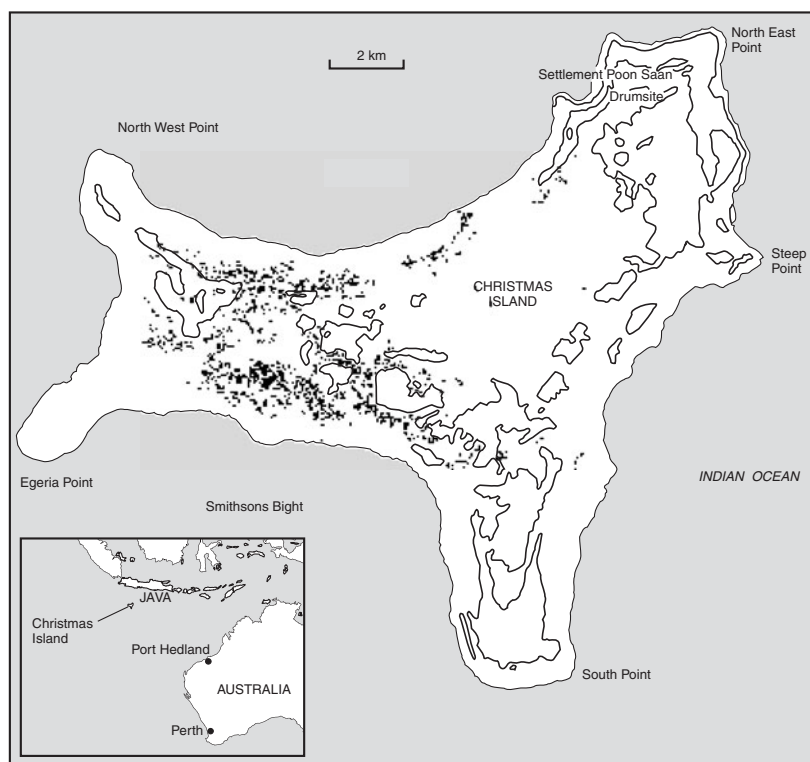
Mainly overlaps with brown and red-footed boobies. At distance best character very distinctive profile, with marked, Concorde-like, forward jutting head and neck, narrow wings, noticeably long in upper arm. Wing beats appear shallow. Closer, black wings plus black-and-white back, white underparts

and black thigh patch diagnostic. Nothing similar in Indian Ocean.

Measurements (see Appendix)

Voice

Silent at sea? At site deep, resonant voice; shouts, grunts, loud, sonorous 'aaw-ah-err'; 'oya-oya'; 'ko-ark, ko-ark' with changes in pitch and amplitude during meeting ceremony. Intimate interactions accompanied by prolonged croaks; may become glottal stops. During copulation, repetitive click-grunts (ancient peleciform vocalization?). In association with special posture, neck at 45°, utters soft, prolonged groan. Large young and juveniles beg with drawn-out, harshly-grating call of 1–2 sec, interspersed with several short, rapid, half-formed throaty sounds, 'ah-ah-ah-ah aa-aa-rr', maintained for hours—distinctive sound of Christmas Island rainforest.



6.59 Distribution of breeding sites (1991), Abbott's booby. (From Yorkston and Green 1992.)

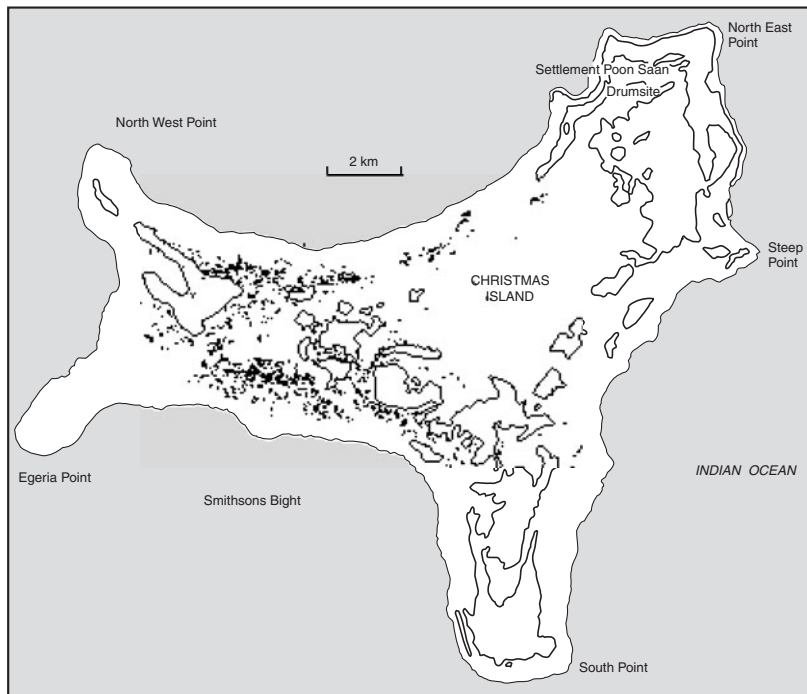
Range and status

Confined to Christmas Island (IO) (Figure 6.59) where collected in 1897 (Andrews 1900). Christmas Island described by Murray (1900) as 'probably the only existing tropical island of any large extent that has never been inhabited by man'. Formerly distributed across IO into W Pacific. In IO inhabited densely forested Rodriguez (Mascarenes) and Mauritius. Bourne (1976) suggests previously on Chagos and Seychelles. W.L. Abbott reportedly collected first specimens on Assumption, but may have been merely roosting (see Nelson 1978b). Fryer (1911) collected specimens there but no mention of breeding.

Steadman *et al.* (1988) have extended previously known range of Abbott's booby by 11,200 km E from Christmas Island into Pacific. Bones of extant form (now *Papasula abbotti abbotti*) on Tikopia in Solomon Islands, 6,400 km E of Christmas Island and an extinct sub-species *P. a. costelloi* on Tahuata

and Hiva Oa, 4,800 km E again from Solomons. Present restricted range due to past persecution. Marquesas settled at least 2,000 years ago and *P. a. costelloi* probably survived into 2nd of these millennia (Steadman *et al.* 1988, Steadman 1989). *P. a. abbotti* may have disappeared from Tikopia soon after human settlement since ages of layers in which it occurred are radio-carbon dated to 2680 ± 90 years BP.

Extensive search of Christmas Island in 1967 revealed 1,844 pairs (counted) 2,300 pairs (estimated) (Nelson 1971, 1978b: 763). Exhaustive survey over several years, first by D. Powell and Kim Chey (Nelson and Powell 1986) then Australian National Parks and Wildlife Service (ANPWS) (Reville *et al.* 1990a; Yorkston and Green 1992; Reville and Stokes 1994) culminated in accurate count of 2,237 'active' (mainly breeding) pairs in 1991, implying total breeding population of *c.* 2,500 pairs. Apparent increase over 1967 figure, despite death of breeding pairs (jungle clearance),



6.60 The distribution of sites held by non-breeding Abbott's boobies in 1991 (Abbott's booby nests either in alternate years or in 2 years out of 3). (From Yorkston and Green 1992.)

due to nests in areas previously missed. Most recent account Yorkston and Green (1997).

Until c. 1970 Christmas Island population little affected by phosphate mining (destruction of trees, removal of soil). Rapid increase in output up to mid-1980s destroyed some booby habitat and perhaps c. 200 breeding adults—serious depletion in species with perhaps lowest productivity of any seabird. Destruction halted in late 1980s but population now operating from reduced base. Probably still viable but vulnerable to natural disasters (repeated cyclones) or changes in availability of food.

MOVEMENTS: Encountered at sea mainly N and W of Christmas Island as far as Chagos archipelago, 4,000 km distant, and in Banda Sea c. 2,000 km NE. Rarely reported; perhaps few observers familiar with it.

Foraging and food

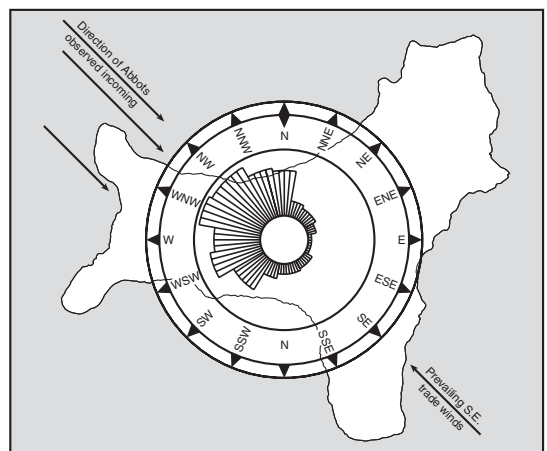
Little known. Not often encountered close to island nor in mixed feeding flocks. May commute directly to distant feeding areas probably NW of island—only direction from which steady stream of incomers approach in late afternoon. Morphology suggests far-forager; egg-size, clutch-size, slow growth and protracted post-fledging feeding support this. But few sightings at sea; returns to island, often at great height, singly, in 2s, 3s or small groups. Probably frequents upwelling off Java; 2 seen at 7°26' S, 105°16' E in August 1974, 330 km NW of Christmas Island (Nelson 1971). Adult female (now in Leiden) shot Sep 1938 c. 405 km N of Christmas Island; in Aug–Oct mass migration of small fish into coastal waters of S Java attracts many seabirds (Becking 1976). At this time Abbott's deliver food to their small young at peak rates and juveniles born the previous year become newly independent; such food flush could greatly enhance survival, reducing excessively long life span which, on breeding data, Abbott's requires. Diet includes flying-fish, squid.

Habitat and breeding biology

(See Fig. at end of ch. 5; Nelson 1971, 1978b; Nelson and Powell 1986; Reville *et al.* 1990a, 1990b; Yorkston and Green 1992, 1997; Reville and Stokes 1994.)

HABITAT: Christmas Island oceanic, of volcanic origin, with superstructure of coralline limestone. Much of 116 km² more than 152 m above sea level. Largely covered with rainforest and until recently almost entirely vegetated and, in parts, unexplored. Most Abbott's nest inaccessibly high in trees, hence pre-1967 lack of information on behaviour and breeding. Breeds in areas mainly above 400–500 ft contours in centre and W of island. Ignores shore terraces and flattest inland areas, though latter contain biggest trees and unbroken canopy. Prefers rugged, dissected parts, providing broken canopy and easier landing and departure; for latter, needs clear 'free fall'. Lands in sub-canopy against wind. Long-winged and web-footed, ill suited to trees, doomed if falls to forest floor. Birds whose nests face NW can enter against prevailing SE tradewinds (Figure 6.61).

Within species-rich climax forest Abbott's strongly prefers *Planchella nitida* and *Syzygium* spp (62.5% of breeding-sites) and *Eugenia gigantea* (Yorkston and Green 1992). *Celtis timorensis*, *Tristiropsis acutangula*, *Ficus microcarpa* and *Pongamia pinnata* and occasionally, *Terminalia catappa*, *Inocarpus fagifer*, *Erhetia javiana* also used. *Planchonella* much preferred (Nelson and Powell 1986), having main branches more horizontal and spreading, giving



6.61 The relationship between compass-bearing of Abbott's boobies' nests, the prevailing wind and the direction from which birds return, after foraging, to Christmas Island. (From Nelson & Powell 1986)

more open canopy for easier entry and minor branches form dense terminal growth providing safer interwoven landing area for newly fledged juvenile.

Most often nests far out among thin, horizontal laterals beneath canopy, but also uses crotches and upper surface of thick limbs; may nest amongst thin uprights. Agile and confident amongst branches. To reach adequate take-off, with free fall, invariably has to bridge gaps of 2–3 m (can turn 180° in single twisting leap) or move along stout limbs using alternate-foot sidle. Uses closed bill as lever but never grasps twig to extricate itself even though grasping used to break off nest-material. Pre-flight, merely lengthens neck, 'peers', makes slight, forwardly inclined intention movements and jumps, sometimes falling several metres until under way. Before landing lowers webs when far out and brakes heavily with wings.

COLONIES: Nests only on Christmas Island; may be tens, scores, or hundreds of metres from nearest neighbour. About 85% of nest trees contain 1 nest, 12% contain 2, occasionally 3. Nesting bird can usually see or hear at least one other pair.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Unique among sulids in that breeding cycle requires *c.* 500 days; thus annual breeding impossible. About 75% eggs laid mid-May–mid-July. Therefore pair lays at intervals of 2 years (see below); some laying, whilst others still tending (by now free-flying) young from egg laid in previous year. Prolongation of breeding cycle through entire year creates severe problems; adults still caring for young in monsoon season (see below).

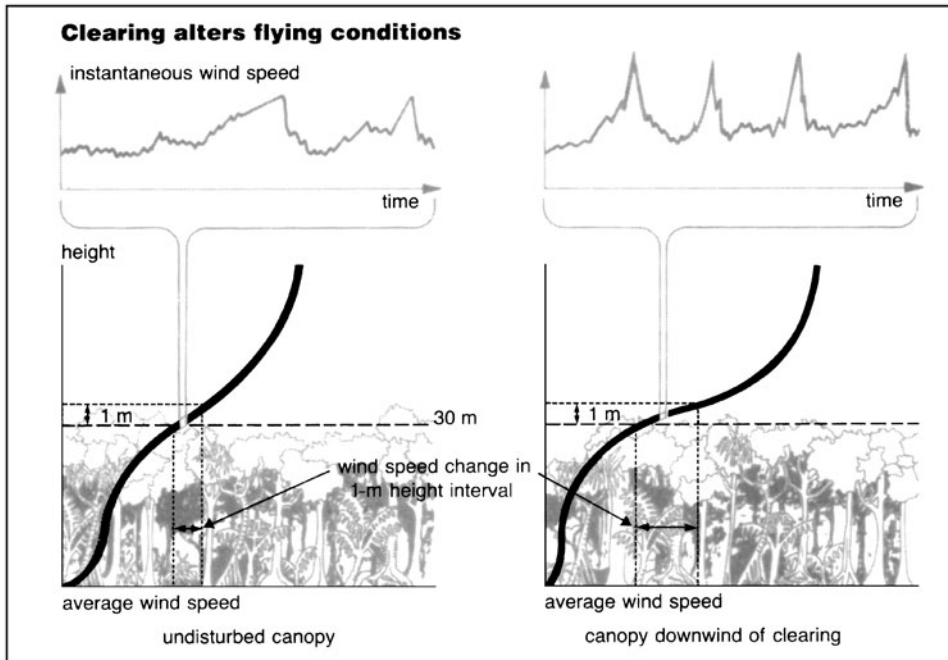
At most, can fit 2 breeding cycles into 3 years; more often once in 2 years. With non-breeding years, lifetime breeding frequency may be *c.* 1 in 3 years. Successful pairs laying in year in which their juvenile departs (18.4%) inevitably lay later. Unsuccessful breeders, mostly losing free-flying young Jan–March, only 25% more likely to lay again that year than pairs whose juveniles departed June–July, but were able to lay nearer to normal time. Almost 30% successful pairs failed to lay in year following departure of offspring but only

18.7% of unsuccessful pairs failed to lay the year after failing. Possibly, release from chick-feeding left such pairs in better condition. Of successful pairs 18.4% thus went straight into another breeding cycle without customary period of nomadism during monsoons. Conversely, many breeders opted out of breeding *even after* 8 months' 'rest' (Aug to Mar). But some had already made 2, 3 or even 4 or more successive breeding attempts. From intensively watched sites, Nelson and Powell (1986) calculated 24.6% pairs opted out after a complete or near-complete cycle (equivalent from larger, less intensive sample 19%). Thus in any one year, *c.* 20% experienced pairs are non-breeders (Figure 6.63). Suggests that even experienced adults avoid incurring stress. In all, Nelson and Powell calculated that, on av, a pair of Abbott's boobies laid 1.27 eggs per 2 years. Theoretical maximum of 1 per 2 years which strict biennial breeding would produce is exceeded because some pairs lay twice in 3 years.

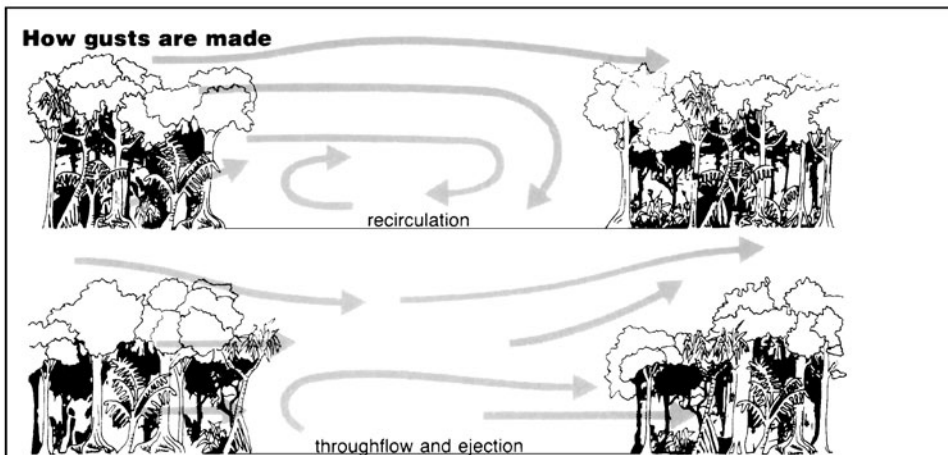
Egg-laying preceded by site-attendance, pair-formation (or re-formation) and nest-building—25–99 (mean 66) days between first return of adult and date of laying. Adults not feeding a winter juvenile return to island around April.

As in anatomy and ecology, social, territorial, and pair behaviour aberrant; adapted to tree-nesting.

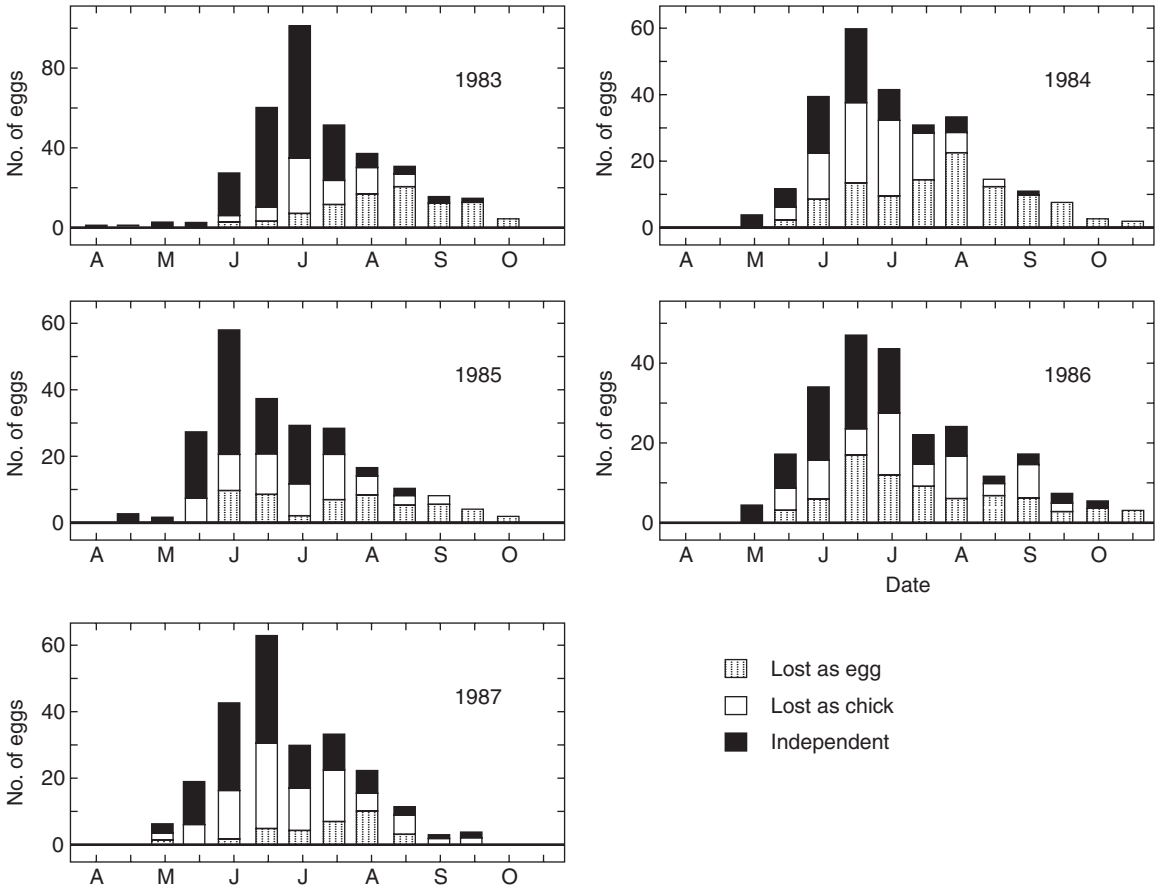
TERRITORIAL BEHAVIOUR: Males repeatedly fly over area containing established pairs. In early stages 'threesomes' not uncommon; always two apparent males and a female (resemblance between adult male and immatures of both sexes raises possibility that one may be offspring from previous breeding). Conspicuously out-posted birds (usually male) attract prospectors. Nest-site selected after initial pair-formation (see below) thus differing from other sulids in which male establishes site and then 'advertises' to females. Defence of nest-site markedly inhibited. Established males generally do not approach closely, or attack intruders; unusually high threshold for overt aggression contrasts with other sulids. Male displaces rival by vigorous display identical to that which occurs between mates. Distinctively oriented towards recipient—a violent,



Downwind of a clearing, Abbott's boobies encounter more frequent and more intense gusts than those in an undisturbed canopy. The sudden change in wind direction and strength — the 'wind-shear' phenomenon so disliked by pilots when landing aircraft — makes flying conditions more difficult and causes dangerous mislandings.



Gusts appear downwind of the clearing when the air suddenly stops recirculating and is ejected into the flow at canopy height.



6.63 Laying dates and subsequent fate of nests, Abbott's booby 1983–87. (From Reville, Tranter and Yorkston 1990.)

spasmodic jerking up and down of head, once every second or two and a shortening and lengthening of neck with vigorous twists and turns. Upward snap of head may take bill into vertical position and as it descends and neck shortens a frenzied mosaic of side-to-side twists and jerks may be vigorous enough to lift bird off branch. As it twists to one side it may lunge forwards. Wings part-open and lifted at high intensity; may remain so for entire bout—several minutes. Tail fanned, head and neck feathers conspicuously raised; displaying bird swallows repeatedly. Head-jerking accompanied by vigorous biting of branch or twig. When performed between mates birds may pull off and hold single leaf or spray. Display is silent. Head-jerking may be vigorously performed even by long-

established pairs with large young, particularly after nest-relief, when outgoing bird head-jerks violently and often bites branches. May occur intensely in male after copulation, when aggression dis-inhibited.

Primarily aggressive but also sexual motivation. Its occurrence at length and (new-pairs) whilst holding nest-material interesting since Abbott's booby lacks special sexual advertising display. Head-jerking strongly reminiscent of head-darting in cormorants and pelicans; may be ancient behaviour which differentiated during evolution but retained basic motor-patterns.

Abbott's other main display 'head-waving' also used in both territorial and pair-contexts, but primarily greeting and bonding (below).

PAIR-INTERACTIONS: Notable feature of pair-formation is absence of any special display by which a male attracts prospecting female (GFA). Potential partners meet simply as consequence of out-posting and aerial reconnaissance. Subsequent interactions establish status and 'intentions'.

Main greeting behaviour—'wing-waving'—sexual and agonistic. Partners display at distance in nesting tree—'in' bird still on nest. Wing-waving slow, powerful beating of wings with backwards-forwards motion, not up and down, wings cambered, shoulder joint loose, often in figure-of-eight movement. Body, *c.* 30° to horizontal, in line with outstretched head and neck, moves vigorously up and down. Movements often lose beat of wings, continue trance-like. Fanned tail moves up and down; head feathers stand on end, greatly enlarging view presented to recipient. Displaying birds shout in deep, far-carrying voice, periodically quietening before rising to new crescendo. Between bouts, stare fixedly at each other. After wing-waving, touch distinctively marked flank in ritualized preening. Performance at a distance rather than contact may be anti-falling adaptation.

Fluctuating aggression/fear during pair-interactions reflected by marked bill-tucking and differences in facial expression (raising or sleeking head and neck feathers) unparalleled in other sulids. Head may be enormously enlarged by raising its feathers, or forehead may remain flat whilst crown rises, or entire head may be smooth with low, sloping forehead. Raised head feathers particularly prominent during head-jerking, wing-waving and copulation but also continuously signal bird's internal state during interactions such as nest-building and change-over. Correspondence between head-feathers and stimulus-shift extraordinarily precise—e.g. at exact instant at which male moves off egg he flattens forehead and raises crown. Even during ritualized (but not in genuine) sleeping when external visual stimuli excluded, head feathers often rise and flatten as internal state shifts. During complicated bout of behaviour head feathers sleek with every act, such as wing-shaking or defaecating, which lacks sexual/agonistic motivation, but are immediately re-erected for next bout of head-jerking and twig-biting. This precise use of head feath-

ers gives Abbott's greatly enhanced signal-capacity. Pattern of head-feather erection in pelecaniforms may have phylogenetic significance; pelicans and cormorants use head-feathers, often exaggerated into plumes or crests, during display.

Ritualized sleeping (conspicuous eyelid, white over middle two-thirds, drawn over eye) unique to Abbott's; cuts off visual stimuli whilst at same time sending a signal. Partners standing close together on nest may screen eye nearest to mate whilst leaving other eye open. Close approach by me elicited closing of nearest eye only. Probably adaptive since close proximity of another individual or of danger could precipitate hasty action and danger of falling. Other evidence shows Abbott's strongly inhibited against sudden flight. A healthy adult will fail to use its wings if thrown into the air but will fly voluntarily if given time to achieve flight threshold. Departure from tree normally very deliberate. In genuine sleeping, Abbott's closes eyes by apposing top and bottom edges of orbital ring, thus hiding white membrane, and puts head in scapulars.

Abbott's entirely lacks allo-preening, both unilateral and mutual. Allo-preening is sublimated aggression; Abbott's internal inhibition of aggression renders alternative mechanism unnecessary.

COPULATION: (GFA)

NEST: Male occupies definitive location before nest begun. After choice of site but in absence of nest-material male and female may perform extensive nest-building movements on *precise* spot where nest to be built. Material gathered by male usually from a distance. Nest substantial, twigs (always green when plucked). Across base *c.* 0.75–0.9 m; moderately deep cup lined with leaves and tips of twigs but never with grasses etc. since Abbott's never voluntarily alights on ground. Nest often incorporates some of branches on which it rests. Later, females pluck material as part of nest-relief. Bird incubating, or guarding young, will accept purely symbolic offering—even single leaf—lift it high into air in conspicuous swinging arc then build it into nest. Monsoon wind and rain, and sometimes cyclones, destroy many nests, leaving juvenile on bare branch.



6.64 Ritualised 'showing' of nest material (cf. blue-footed booby which builds a merely symbolic nest but also 'shows' nest material).



6.65 The single egg of Abbott's booby is a higher proportion of the female's weight than in any other sulid.

EGG/CLUTCH: 78×51 , 100.5 g; 84×54 , 124 g; 82×53 , 112 g; (6.9%, 7.6%, 6.7% female weight). Both absolutely and as % of female weight, Abbott's egg heavier than any other sulid. Egg loses *c.* 11% weight during incubation. Clutch always one.

REPLACEMENT LAYING: Not usual but occurs.

INCUBATION: Shared. Egg incubated beneath or on top of webs; shaded during heat. Tends to incubate back to sun. Often click-grunts as changes position by 90 – 180° . Nest-relief preceded by display, beginning as incomer lands in outer branches and continuing as approaches nest. Soft click-grunt as settles on egg. Close proximity of mates accompanied by erection of head feathers and on occasion by bill-touching or jabbing and brief wing-waving, followed by displacement preening of thigh-patch or wing-bow. Slow withdrawal of outgoing bird accompanied by head-jerking or twig-biting. Departure from nest often preceded by curious forward crouch, sometimes horizontal, and motionless for up to a minute. Departing bird 'wing-rattles' before flying. Once on nest incomer 'nest-builds' and ignores mate. Frequently preens and oils feathers.

Incubation period *c.* 57 days; longer than any other pelecaniform except frigatebirds. Male shifts 7–95 hr (av *c.* 55 hr); females 16–119 (av 50 hr). Details for first 39 days' incubation at one nest: male 7 shifts (71, 24, 72, 25, 95 and 7 hr), female 8 shifts (31, 48, 50, 96, 119, 24, 16 and 24 hr). Female took first shift after laying. Av for both sexes over entire period *c.* 48 hr.

CHICK: Starring to emergence, 36–48 hr. Hatchling has thicker down than other sulids. Eyes open first day. Skin purplish, bill lead grey with black tip; white egg-tooth. Feathers of greater wing-coverts which, with scapulars, later form distinctive black cape, begin to show at 15–20 days. Down on humerus and radio-ulna displaced by brown-tipped feathers which seem mainly transitory though some juveniles retain few small brown scapulars. After 30 days black edges develop on grey webs; orbital ring blackens. At *c.* 31–7 days forehead clears of down; wide band of bareish skin extends beyond eyes ending sharply where down of crown begins. This bare area, which precisely corresponds to that which adults can flatten whilst keeping other head-feathers erect during display, develops short, buff-tipped feathers in two fan-shaped tracts, apices



6.66 Abbott's booby chick differs from all other sulids in the nature of its first downy plumage and the formation of a black 'cape'. Note the conspicuous eyelid of the adult.



6.67 10 week-old chick with parents. Note that whereas the adult, by drawing its eyelid across had 'cut off' the sight of its partner (to reduce aggression-eliciting stimulus) the near adult has not 'cut-off' the chick.

pointing forwards. The tips abrade, or the feathers are soon replaced, since fully grown young have pure white heads like adults. These buff-tipped tracts appear to be only equivalents of brown juvenile plumage found in all other sulids. At 40–50 days down on body extremely thick, short and woolly (Figure 6.66) more like a pelican or cormorant chick's than longer, fine down of other sulids. Down on head and neck extremely long with deeply dissected tips giving distinctively loose appearance. Primaries emerge days 46–50.

As black feathers on wings and scapulars extend young Abbott's resembles miniature adult and further growth transforms it into juvenile closely resembling adult male, which explains why juvenile undescribed until Nelson (1971). Bill turns pale grey-blue, slightly less vinous than adult male.

Growth extremely slow. By 10 weeks only 90% adult weight; brown booby, same island, adult weight *c.* 7 weeks. First 3 weeks' growth particularly slow which may reflect unusual feeding habits of chick. Free-flying young may drop below 50% adult weight. At fledging weighs *c.* 85% adult.

CARE OF YOUNG: Broods or guards continuously first 4–6 weeks; thereafter, up to a few hours on

each visit. Because of slow development, chick thus exposed whilst still vulnerable, but nest inaccessible to predators with significant exception of Christmas Island sparrowhawk (*Accipiter fasciatus*). At first, adult cleans and probes nest-cup and flings fragments of spilt food away. May preen chick. Uniquely among sulids, may (during first fortnight) deposit food into nest cup though difficult for small chick to pick up. Adult may re-swallow and regurgitate several times, softening and fragmenting bolus. Later uses normal sulid method of incomplete regurgitation. When nest disintegrates during monsoons, chick or juvenile fed only on *precise* site of nest. Most adults return late afternoon or early evening; not in darkness. Frequency of feeds steadily decreases and by mid-monsoon season, when juvenile free-flying, may be extremely irregular and infrequent. Juvenile remain at site almost continuously, yet weeks may elapse with only one or two parental visits. At best, each parent may visit once in 2 days. Great variability between adults in feeding frequency, indicating importance of experience and mate-compatibility in ensuring breeding success, though climatic conditions also crucial. As juvenile's departure draws near it is fed more often than in wet season. On occasion, such juveniles refused feeds. Since it has

by then been free-flying for 6 months, has practised fishing and may be proficient.

BEHAVIOUR OF YOUNG: At first, begs by gently jabbing base of adult's bill or nibbles its breast feathers whilst calling repetitively. Stylized begging develops at 4 weeks and is retained until end of post-fledging dependence. *Contra* other boobies, marked by considerable restraint even *in extremis*. Hunches head between shoulders, bill pointing downwards, and sways it rhythmically, uttering repeated 'qua-qua-qua' followed by prolonged grating call during which it brings head forward and down. Wings raised from back or variably spread and resettled but not waved or flailed. Does not touch adult. Even quite small chicks defaecate over rim to avoid fouling nest. Have marked appeasement posture, hiding bill beneath body. Adult-type bill-tucking appears at c. 5 weeks. May rest and sleep prone. Precursors of adult territorial display, head-jerking, noted in 7-week-old chick with no adult present but greeting (wing-waving) not seen, even in juveniles.

Between hatching and just before first flight youngster does not leave nest (or site if nest falls apart) but when ready to fly it moves to suitable take-off point in canopy. After first flight juvenile has obvious difficulty returning to site in nesting tree. Some fall either to forest floor, where doomed, or land in lower branches from which they must climb upwards. If epiphytes present, young booby levers itself upwards and uses claws and wings, but never grasps foliage (same technique as displaced gannet chick, though ineffective in twigs). Fallen youngsters not necessarily weak; several restored to their tree eventually departed successfully.

FLEDGING: Between first flight and final departure, c. 6 months, juvenile makes short sorties over island but rarely absent for >1–2 hours, minimizing risk of missing parental feed which could be critical. Thus gains only limited foraging experience before quitting island. Even shortly before leaving, did not spend increasingly long periods away from tree (present 86% of daily checks in 6th week before leaving, 87% (5th), 82% (4th), 84% (3rd), 83% (2nd), 79% one week before).

Fledging period 151 days (140–75) $n = 11$; 30–50 days longer than any other sulid. Contributory factors are slow growth (infrequent feeds but also adaptive slow development) and need for juvenile to defer first flight until competent (practice too dangerous). Fledges Aug–Mar; c. 78% Dec–Jan.

POST-FLEDGING: Free-flying juvenile dependent on parents for 230 (162–280) days. Great spread partly due to spread of laying. Thus some young enter monsoon period less well-developed and then need longer period to attain condition adequate for independence. Also, severity of monsoon's effect on food varies. Most departures from island July–Sep. Fledging and post-fledging periods total c. 363 days (314–418) $n = 22$. Complete breeding cycle av c. 486 days.

BREEDING SUCCESS: Hatched from laid: c. 72.7% ($n = 1,322$, ANPWS, underestimate, chick not detectable <3 weeks). Fledged from hatched: 74.1% ($n = 962$, overestimate because of undetected deaths of chicks around hatching). Fledged from laid, variable: 10–50%, usually 30–50%. 26% ($n = 265$, 1974–80), 33% ($n = 109$, more intensively studied sample, Nelson and Powell 1986); 51% (1983), 24% (1984), 45% (1985), 37% (1986), 44% (1987), av 41.1% ($n = 1,322$, ANPWS, using different methods). Variability mainly due to natural disasters (cyclones, oceanographic influences) and social composition of year's breeding population. For example, in 2 pairs mates remained together for 6 years without rearing any chicks, another reared 1 chick in 8 years whilst 2 pairs each reared 3 chicks in 5 years. Failure occurs mainly around hatching and (massively) between first flight and independence. Feeding rate lowest Jan–Feb, highest Oct. Starvation Dec–March, caused 63–84% of deaths verified by weighing dead or fallen young. In 1977, 45 deaths in March, 8 in Feb, 1 each in Jan and April. Between 1978 and 1980 Feb main month of starvation (7 cases), Jan (4), April (3), March (2). Violent winds blew juveniles out of nest or off perch. Cyclone Sue (13–14 Dec 1975) blew down 9 free-flying juveniles from 46 occupied nests, representing massive mortality. 27 deaths Dec 1975 were of part-grown young (24 aged 2–5

months). Cyclones may follow in quick succession, as in late 1974 and early 1975, occasionally as late as May. First half of breeding season may suffer abnormally heavy rain. In Sep 1975, usually driest month, 3,460 mm of rain, 4,745 mm in Oct; many nests disintegrated and young killed. In March 1988 cyclones felled about a third of trees holding monitored breeding-sites, killing 30% fledglings (Reville *et al.* 1989). Could reduce breeding success to below 10% and lower subsequent success by delaying next cycle.

Abbott's booby adapted to regular seasonal oceanographic events which underly breeding regime. Reville *et al.* (1990a) demonstrated regular annual fluctuations in sea-temperature; in Jan sea-surface temperature rises sharply from a basal *c.* 26°C to *c.* 29°C, or more. This reduces food in Abbott's foraging area since base of food chain depends on cold, nutrient-rich water brought to surface as result of SE Trades which blow from *c.* May–Oct; primary productivity much higher during months when sea cooler. Seasonal changes mean food most readily available when Abbott's feeding small young which require constant presence thus reducing adults' food-gathering capacity. Time-lapse photography showed feeding rates highest in Oct. But exceptionally slow growth of chick means that even if fledges by Dec, only options are to remain dependent on parents throughout monsoon, or attempt independence at this unfavourable time. Despite attendant mortality, Abbott's has chosen former.

PRODUCTIVITY: Powell (Nelson and Powell 1986) showed 109 pairs reared 70 juveniles to independence during 9 years or 0.111 per pair per year, thus 9.1 years to produce one juvenile. Lowest comparable figure for any other sulid is *c.* 1 in 2 years. Thus even least productive of other sulids nearly 5 times more productive than Abbott's whilst, normally, Peruvian booby *c.* 25–30 times so. ANPWS show that over 5 years 1,322 pairs reared 543 young to independence, or 0.082 young per pair per year thus requiring 12 years for a pair to rear one offspring. Since some independent offspring die before breeding, it requires more than 24 years for breeding pair to replace itself. Reville *et al.*

(1990a) conclude 25–31 years. This assumes high survival of juveniles after leaving island, possible if, during 6 months of free-flying but subsidized life, young Abbott's become proficient. But free-flying juveniles spend 70–90% of time in nesting tree, awaiting arrival of food-bearing parent.

FIDELITY TO COLONY, SITE, AND MATE: Since Abbott's endemic, all birds return to Christmas Island to breed.

Probably highly faithful to site and mate in successive breeding attempts (Nelson 1978b). Returns, April–May, straight to site of former nest. Such birds probably established pair. Strong disadvantage in establishing new site and mate. Old site unlikely to have been taken over by another pair, since Abbott's nest well dispersed and sites plentiful. Site fidelity provides valuable continuity after rest years. Christmas Island contains many hundreds of non-breeders (Figure 6.60)—pre-breeders and experienced but non-breeding adults distributed within areas occupied by breeders (Yorkston and Green 1997). Do not congregate in clubs or loafing aggregations.

AGE OF FIRST BREEDING: Probably long deferred.

NON-BREEDING YEARS: Low frequency of breeding attempts due to unusual breeding cycle further lowered by intermittent 'rest' years. Frequency probably variable (Nelson and Powell 1986).

LONGEVITY AND MORTALITY: Evidence (above) that a pair rear one independent offspring every 10–12 years, some of which die before breeding, means extremely low adult mortality if population stable. Even if all independent offspring survived to breeding age, would take 20–4 years for breeding pair to replace itself. Given 25% pre-breeding mortality would raise adult life expectancy to 25–31 years. Av life span likely to exceed this; possibly 30–355 years.

ANPWS suggest adult mortality (1983–88) 4.5% but this figure artificially high because turbulence associated with man-made clearings caused higher than natural mortality (5.4% against 3.2% for birds far from clearings). Nelson and Powell

suggested adult mortality rate of 4% or less if population to remain stable. ANPWS, on their recruitment figures and likely adult mortality (including extra associated with clearings) imply population

declining, but would do so even at 3.2% adult mortality. Unfortunately, surveys in 1991 found 36% of population was in areas affected by clearings (Yorkston and Green 1997).

Red-footed Booby *Sula sula*

PLATE 4

Pelecanus sula Linnaeus, 1776, Barbados, West Indies.

Binomials have included: *P. piscator*, *Sula piscator*, *S. piscatrix*, *S. rubripede*, *S. erythrorhyncha*, *S. brasiliensis*, *S. candida*, *S. hernandezii*, *S. coryi*, *S. websteri*, *S. nicollii*, *S. autumnalis*, *S. cyanops*, *S. fiber*, *Dysporus piscator*.

Other common names: red-faced booby, red-legged gannet, white booby, tree booby, Webster's booby, brown booby. Many local names, Malaysia, SW Pacific.

French: fou à pieds rouges, fou bête (Seychelles). German: rotfusstolpel. Spanish: piquero patirrojo, pajaro bobo blanco.

Sub-species

(Details, with illustrations in Nelson 1978b: 658–65.)

Several colour-morphs (*not* 'phases') often coexist and sabotage attempts to demarcate regional sub-species. *Sula sula sula* (white form: brown with white tail) occupies type-locality (West Indies) and occurs South Atlantic. *S. s. rubripes* (mainly all white) Indian Ocean eastwards into extreme W Pacific though on Europa (Mozambique Channel) adults are brown with white tail and on Tromelin (W Indian Ocean) one-third are brown with white tail, two-thirds all white (a constant ratio for at least 40 years, Le Corre 1999) whilst on Wallis and Futuna (SW Pacific) 54% are brown with white tail and only 27% all white (Gill 1995). *S. s. websteri* (all brown; brown with white tail; all white; white with black tail) E Pacific N to Revillagigedos. Would be absurd to treat colour morphs as distinct sub-species and even more so to describe one of

commonest brown morphs (brown with white tail) as a distinct species, *Sula nicollii*. Problem is selectively unpenalized poly-morphism, partly divorced from regional influences. Even recognition of 3 sub-species listed above means that white morph from Galapagos, *S. s. websteri*, and that from Christmas Island (I O) are supposedly distinct, even though less different from each other than, say, white morph and part-dark morph which breed on Canton Island or white and brown morphs on Tower (Galapagos).

Description

ADULT M PRE-BREEDING: White morph, commonest form, plumage all white except for yellowish head and neck (depth of colour variable); general plumage sometimes tinged cream or yellow. Blackish primaries, secondaries, some wing coverts with variable 'frosting' on outer webs. Bases of secondaries white. Tail white (commonest) or blackish according to region (e.g. white I O, black parts of P O). Brown morph can be uniformly warm brown with slightly darker primaries and secondaries, but wide range of shades results from differential fading. Together with regional variation give individuals from extremely pale, through gingerish to deepest brown. Heads of brown morph breeding females go streaky. Some brown morphs (e.g. West Indies) have white tails, others (e.g. Galapagos) brown tails. Bill blue, face often reddish but sometimes greenish with some orange or pink. Gular skin black. Eye brown, grey, chestnut or yellowish with (usually) blue orbital ring. Legs and feet rich crimson through purple-red to pale red, sometimes slightly orange. Claws greyish or pinkish. Regional variation in soft part colours.



6.68 Brown morph and black-tailed white morph of the red-footed booby, in the Galapagos.



6.69 White-tailed white morph, Christmas Island (IO).



6.70 Late immature white morph, Christmas Island (IO).

ADULT F: Similar but larger.

POST-NUPTIAL: Little change; in brown or partly brown morphs ageing gives paler edges to wing coverts. Facial and leg colours duller or may change hue.

JUVENILE AND IMMATURE: Newly fledged, darkish brown with darker primaries, black bill, blackish facial skin, light greyish or yellowish iris and dark grey, khaki, orange or puce feet. *En route* to adult plumage acquire mottled, grey-brown heads, variably grey-brown or mottled back and wings,

brownish tail, increasingly white underparts. Bill and feet dirty shades through blotched and dull colours to adult hues.

Field characters

Blue bill and red feet diagnostic of adult. White morphs distinguished from masked booby by smaller size, absence of black humerals, white innermost wing feathers (tertials)—black in masked. Differs from African and Australasian gannets by white tail, red feet, and smaller size. Immature not readily distinguishable from all possible plumages of immature masked, brown, and blue-footed boobies, with all of which it may overlap, or from gannets, though 'jizz' distinctive, but combination of following helps: bill black or turning bluish; feet khaki or puce; small size; absence of white patches anywhere and of sharp demarcation lines; absence of specific features of potentially confusable species, such as brown booby's diagnostic underwing or blue-foot's white nape patch.

Measurements (see Appendix)

Voice

Rapid, brassy inflying notes apparently rising in volume before dying away 'rah-rah rah-RAH-rah-rah'. Sharp 'karr-k' from molested bird. Males call, rising and falling, when moving within territory. During copulation male utters harsh, drawn-out note (no other sulid does so). During sky-pointing male again utters rasping call instead of whistle of some other boobies. Young birds beg with passionate, rapid 'chuck' call, rising and falling.

Range and status (Figure 5.14, 5.15)

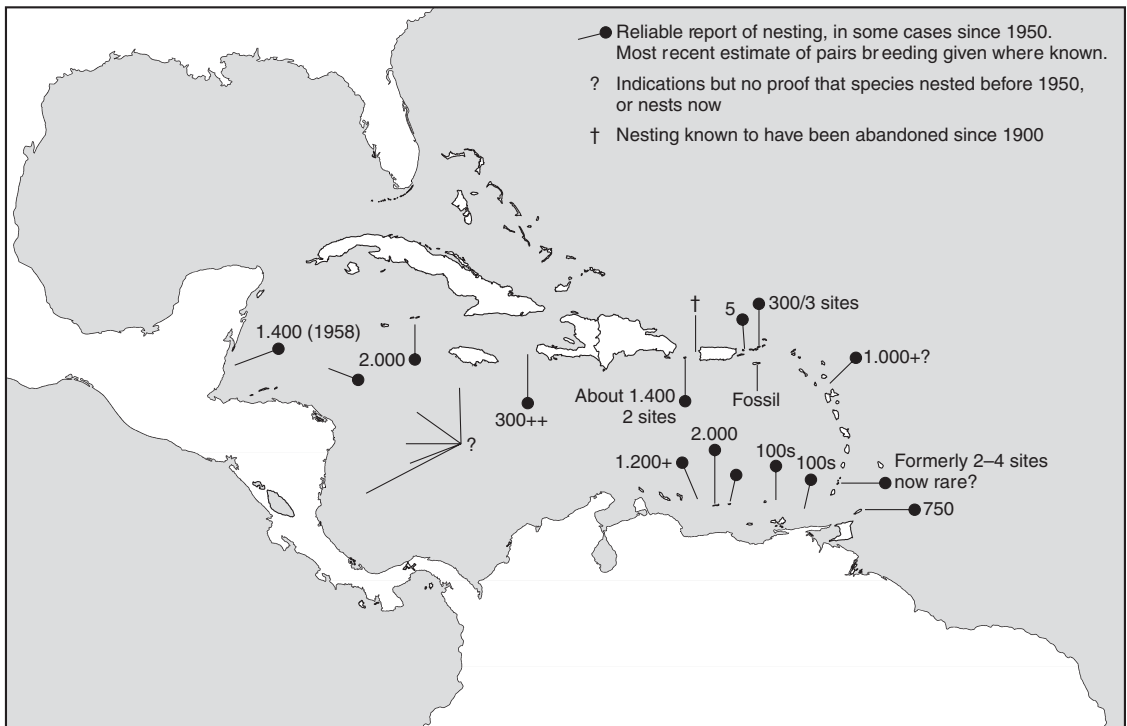
Pan-tropical, breeding widely in 3 major oceans *c.* 17°N–26°S. Highly pelagic; seen far beyond breeding range. Often sympatric with masked and brown and with main kleptoparasite, great frigatebird. Schreiber *et al.* (1996) provide most recent figures for world population (345,000 pairs). In all areas their guesstimate substantially lower than mine (Nelson 1978b) and probably better.

Caribbean population much decreased in recent decades; estimate puts population at less than some

single-island populations in other parts of range. However, Little Cayman held *c.* 5,000 nesting pairs in 1997, 30% of entire Caribbean population (Burton *et al.* 1999) on which basis Caribbean holds *c.* 16,700 pairs. Atlantic Ocean no longer hosts a single large colony. Indian Ocean continues a major stronghold. Schreiber *et al.* (1996) estimated a mere 26,000 pairs, probably below true figure. Unlike Atlantic, tropical Indian Ocean full of archipelagoes, with tens, hundreds, or even thousands of islands and islets, many sufficiently vegetated for red-feet. Aldabra *c.* 6,000–7,000 breeding pairs (Diamond 1974). Europa, Mozambique channel, *c.* 2,800–3,800 pairs (Le Corre and Jouventin 1997b). Seas N of Australia similarly provide islands, but little information.

Pacific may hold most of world population, and Galapagos has largest single-island one. Cays of Great Barrier Reef hold colonies, though comparative lack of vegetation makes many more suitable for ground-nesting brown and masked boobies, and man has reduced population. Nevertheless, recently established colony on Adele Island (Coate *et al.* 1994). Large colonies (10,000 pairs?) Manok Island, Banda Sea (Simpson 1970). Further E, much of W Pacific depressingly depopulated of red-feet, though some small pockets, as in Fiji. Apparently large colonies on Surprise Island (New Caledonia) (Robinet *et al.* 1997). No central Pacific island now holds large numbers, though several support in the low thousands of individuals and a few—e.g. Palmyra, Millenium (Caroline)—significantly more; Caroline *c.* 7,000 birds (Kepler *et al.* 1994). In tropical E Pacific, dearth of suitable islands. Forested Cocos Islands hold substantial numbers and Galapagos archipelago may host 250,000 pairs. Because less accessible to man, this is probably most abundant sulid, though world population fell by probably hundreds of thousands in 20th Century.

MOVEMENTS: Adults disperse widely. Young leave colony before 1 year old and do not return until 2 or 3. Only 1% of 2,377 chicks ringed on Johnston Atoll recaptured as subadults there (Schreiber *et al.* 1996). May congregate on islands where do not, or are not breeding. Juveniles and immatures may gather in small groups with low-intensity agonistic behaviour. Move widely between islands in north-central Pacific. Up to 60% ringed



6.71 Breeding distribution of the red-footed booby in the Caribbean (c14,000 pairs). (From Halewyn and Norton 1984.)

birds, recaptured, had been ringed as adults or young elsewhere. May be vast areas over which population essentially one gene pool.

Foraging and food

Pelagic; often, especially juveniles, encountered far from land. Voyage between Tahiti and Kiritimati logged 1,878 red-feet, exceeded only by sooty terns (Phillips and Wragg 1993). Furthest from land *c.* 340 km and 86% within 200 km. Ballance (1995) found 6 boobies from Johnston Atoll had av 3.8 trips to sea over 3.21 days, 84% of time in flight, 12.4% sitting on water. She gives, also, data on the energetics of foraging. Most red-feet leave colony at daybreak but may depart any time of day, often in loose groups—scores of birds including juveniles. Often soar in updraughts. Flies at *c.* 46 kph. Feeds singly or in flocks of up to several hundreds with terns, shearwaters, and other booby species. Converge over shoals driven to surface by predators

such as tuna. Long wings and tail and lightness make it agile and adept at taking flying fish in flight or near surface; their wing loading is lower than would be predicted from mass alone (Hertel and Ballance 1999). Dives headlong from at least 7 m and said to penetrate up to 8 m. Le Corre (1997) recorded mean max depth of 4.9 ± 2.0 m (range 2.9–9.7). Must use feet and/or wings to reach max depths. Has larger eyes than other boobies (except Abbott's) and notably crepuscular, often returning long after dark even on moonless nights (personal observation) and perhaps hunting at night. Returning boobies often chased by frigatebirds. On Europa, Le Corre and Jouventin (1997b) found that 0.5–1.0% of returners regurgitated to great frigatebirds. Birds returning in group or flying more than 50 m high, or after dusk, less likely to be chased. On Tromelin, where frigatebird pressure lower, boobies less prone to return after dusk.

Flying fish and squid major prey. Most items 50–100 g and 10–22 cm (mainly 6–15). Fish taken

include *Exocoetus* sp, *Cypselurus furcatus*, *Oxyrhamphus micropterus*, *Hemioramphidae* and *Gempylidae*. Squids (in Hawaii all 5 Ommastrephidae) formed 36% of diet by volume (Ashmole and Ashmole 1967), 27% (Harrison *et al.* 1983); Christmas Island (P O) 25% (Schreiber and Hensley 1976); Aldabra (wet season) fish 79% by weight, squid 21%, dry season 99% fish (Diamond 1974).

Habitat and breeding biology

(See Fig. at end of ch. 5; Nelson 1978b.)

HABITAT: Prefers small oceanic islands or perimeter of larger ones though will breed several km inland. Largely arboreal, in low scrub or high in tall trees, but can use cliffs or even ground (but hesitant and awkward because of short tarsi). Most commonly builds at 5–10 m but up to nearly 30 m and beneath canopy. Mangroves, *Pisonia* and *Turnefortia* well favoured but many other trees used. Perches expertly; hops with both feet together. Uses bill to lever (but not grasp) out of awkward situation.

COLONIES: Typically traditional; highly variable in size, nests usually well-dispersed but may be several per tree. Expressed as pairs per 1,000 m² ranges from few to (exceptionally) several hundred (Nelson 1978b, Schreiber *et al.* 1996). Division into 'groups' or sub-colonies usually evident.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually, but exceptionally, as some years in Galapagos, slow development and protracted post-fledging care, lengthens breeding cycle and then breeds less frequently than once a year. Loss of mate may lengthen interval between breeding attempts. Generally loosely seasonal, but considerable spread of laying and sometimes two or more widely separated peaks. Main laying months vary with region. In many, such as Aldabra (IO), Caribbean, Galapagos (PO), birds present at colony every month and may be several bursts of laying; Tromelin (IO) may lay in any month. Elsewhere, as on Christmas Island (IO) laying largely restricted to April–June. Sub-group synchrony may be marked. Good evidence that in Galapagos timing

of laying determined by food acting as proximate trigger (Nelson 1969). Here unpredictability of food rules out strongly seasonal laying linked to reliably abundant food at chick-rearing stage, but leaves option of producing egg when feeding favourable.

TERRITORIAL BEHAVIOUR: Influenced by arboreal habit. Repeated territorial flight circuiting terminates in ritualized in-fighting, tremoring wings held in V, rapid 'rah-rah-rah' call. Fighting brief and infrequent—stabbing, bill-gripping, and wing flailing, with screech; 'sparring' (head flick with open beak); ritualized display (forward head-waving). In latter grips or bites twig, swaying from side to side and vocalizing; probably redirected aggression. Territorial behaviour less stylized than other boobies and confirms phylogenetic disparity.

PAIR INTERACTIONS: Partners hostile; sometimes overt attack by male; jabbing and sparring common. Locomotion difficult in trees, which reduces mosaic of interactive behaviour. Male 'sky-points' to attract female; lengthens neck with prolonged greeting call, points bill upwards, raises tail, and raises wing tips keeping wings closed. Thus two wing-tips, tail, and bill all point upwards (four pointing). Partners in close proximity may sky-point alternately but not simultaneously. Female responds to male jabs with low-intensity fear—neck-tremoring with ruffed head feathers, flinching, and facing away. Sky-pointing homologous with other sulids. Wing-flicking (flight-preparation) particularly noticeable in red-foot. Also 'wing-rattle', shaking loosened and slightly raised wings. During hops, arches neck and points bill down.

COPULATION: (GFA)

NEST: Typically partly sheltered by canopy or vegetation. Usually in living trees with favourable access and departure (wind and drop), occasionally on cliffs or even ground. At flimsiest, frail platform through which egg could be lost but usually solid base with shallow cup lined with finer twigs; often incorporates leafy sprays. Built mainly by female; material brought

by male. Twigs placed to one side and quivered. Most intensive in pre-laying phase of frequent copulation and prolonged attendance. Nest-building movements common during courtship even when no nest, and as displacement activity during conflict behaviour. Digs into bottom of nest and flings away items which could damage egg. Typically 26–45 cm diameter with outside depth 7.5–18.0 cm, sometimes grows massively over years. Height 0–30 m. Often dismantled by free-flying juvenile.

EGG/CLUTCH: Elongate, slightly broader at one end. Chalky outer layer *c.* 0.4 mm thick. Shell thickness pre 1947 1.91 mm *n* = 15; from 1951–65 1.86 mm *n* = 5; difference not significant (Morrison 1979). Shell light blue, bluish-green or bluish-white but sometimes pinkish. Measurements: Caribbean 59.4 (53.3–72.2) × 39.8 (36.7–48.7) *n* = 100; Christmas Island (IO) 59 (54–63) × 39 (36–41.5) *n* = 6; Tromelin 57.9 (52–63) × 38.2 (37–42) *n* = 11. Weight: Caribbean 47.1 (35–58.3) min weight, partly incubated; Christmas Island (IO) 47.3 (40–54); Galapagos 54 (41–66) *n* = 48. Galapagos egg *c.* 5% female weight but less on Christmas Island (IO). No seasonal or annual difference in weights on Christmas Island (PO) (Schreiber *et al.* 1996). Clutch invariably one.

REPLACEMENT LAYING: 10–40 days; after large-scale natural loss only small number replace. Older birds lay 2nd or even 3rd time more often than do first-time breeders.

INCUBATION: Female may spend several days continuously at nest before egg laid. Incubation shared; begins minutes or few hours after laying. Male usually first long stint. Shifts vary with region, 1–6 days: British Honduras 24 hr; Johnston Atoll 24; Aldabra 37; Christmas Island (IO) 53; Galapagos 60. Where food unpredictable, such as Galapagos, off-duty birds may be unable to shorten foraging stints and hatchling may starve. Probably in response, particularly in impoverished areas, egg has large food reserves (Nelson 1969). Incubation period: Galapagos (PO) 46 days; Johnston (PO) 45.4; Caribbean 44.5; Christmas Island (IO) 45.

CHICK: Hatchling *c.* 120 mm, bill 17 mm, weight 35–40 g. Pink, mauve, grey, or purplish with blackish bill and dark grey feet and legs. Eyes open day 1–2, iris dark brownish, light grey or (later) yellowish. Day 7–10, covered short white down on back and posterior margin of wing. Day 21–8 down spreads, thickens, and lengthens. Later development varies with region and conditions. Where favourable contour feathers, primaries, rectrices, and scapulars visible end week 6, secondaries appear week 7 and by week 8 most of back covered with feathers. Weeks 9–11 feathers replace down over breast, upper belly, and lower back, and by end week 11 wings may be clear of down and pectoral band plainly marked. Appreciable down remains back of head, neck, rump, belly, and thighs until at least week 13 and wisps until week 15 (week 20 or beyond in Galapagos). By then general plumage dark brown, primaries and secondaries blackish with hoary bloom, tail dark brown with paler tips and shafts. Feet khaki, pale orange, tomato or puce. For growth curves see Figure 3.11. When fledges may be slightly heavier than adult with slightly shorter wings.

CARE OF YOUNG: Eggshells left on rim or dropped over. Chick brooded on webs first few days; then brooded or attended until 4–5 weeks when can thermo-regulate and release parents. Nest-relief brief with jabbing and facing-away (female). Often, sitting bird merely rises and departs. Male may fetch nest-material. Adult stimulates hatchling to feed by repeatedly touching its head, or chick periodically raises and moves head, ruffling adult's breast feathers and stimulating it to regurgitate. Later, chick begs frenziedly as adaptive response to food-shortage (adult may be reluctant to disgorge, though if crop full usually eager and begins to regurgitate before chick contact). Bout of feeding 1–6 successive entries and chick fed *av c.* 1/day after *c.* 4 weeks old. In Galapagos feeds infrequent during unfavourable periods and much starvation. Adults return mainly late afternoon and evening, also early morning. In Galapagos, weights of feeds (from 3-hourly weighings of chicks): up to 50 g (2), 51–100 (6), 101–50 (9), 151–200 (10), 201–50 (9), 251–300 (3), 301–50 (1), 451–500 (1) (Nelson 1969). Probably *av c.* 200 g which compares with *av* 149 g for Aldabra (Diamond 1974). In neither case



6.72 Adult white morph with 8 week-old chick, Galapagos.

possible to rule out weight increases due to feeds from both parents. Av weight daily feeds Johnston Atoll: chicks 1–3 weeks 37 g, 4–7 weeks 115, 8–11 weeks 200 (Schreiber *et al.* 1996). Until young can fly, adults do not usually discriminate between own and others; chicks accept foster parents or siblings. Later, adults repel strange young.

BEHAVIOUR OF YOUNG: Heat-stress can be severe. Adopts special posture with bill spiked into nest bottom and dilated cloaca elevated to radiate heat. Excretes onto webs for evaporative cooling. May dangle head and neck or incline head upwards and flutter gular skin. Sleeps prone on nest. After week 4 may climb onto exposed perch and exercise wings. From *c.* 5 weeks attempts to defend nest against intruding adults of own or other species. Lacks prone, bill-hiding posture of other sulids and although adults of own species avoid youngsters who attack them, adult masked boobies may kill them. When fully grown, presumed male chicks show adult-type territorial behaviour, displacing intruders and performing site-ownership display. Whilst still dependent may join other juveniles near breeding area and shows strongly agonistic (fear/aggression) behaviour.

FLEDGING: 14–17 weeks, depending on region, fully feathered and capable of flight. May try short practice

flights. Fledging period long for a booby. Aldabra *c.* 110 days; Caribbean, 99–112; Christmas Island (IO) 100–110; Galapagos up to 135+. Two exact figures for latter 135, 136, >6 weeks longer than some Caribbean birds. Loses weight before fledging.

POST-FLEDGING: In Galapagos 11 free-flying juveniles fed for 78–103 days. Elsewhere indications that *c.* 30 days (possibly 60–90) may be usual.

BREEDING SUCCESS: (Galapagos, Nelson 1969; Kure, Woodward 1972; Honduras, Verner 1961) Hatched from laid: 30–70% (excluding man), perhaps as high as 90% (Honduras). Fledged from hatched: 28–95% (differing by area and year). Fledged from laid: up to 80% (Kure, several years, several groups); at least 70% (Honduras); 8.4% (Tower, Galapagos, 1964, but this year adversely affected by ENSO). First-time breeders less successful than experienced; 40–50% against 73–80% in birds more than 8 years (Hawaii; Hu 1991). Assuming moderately high productivity (65%) for 15 years and 50% pre-breeding mortality, a pair would recruit 4 breeders to the population. But in many areas man grossly reduces this figure; collecting eggs, killing adults and young, and tourism which causes loss of eggs and small young to, e.g., frigatebirds. Some interference from conspecifics but probably not significant. Main cause of death where chick mortality high, as in some years in Galapagos, is starvation. Predators include (Galapagos) hawks, short-eared owls, and frigatebirds. Elsewhere, introduced pests as well as natural predators.

FIDELITY TO COLONY, SITE, AND MATE: Recapture of large numbers ringed in POBSP (Woodward 1972, Schreiber *et al.* 1996) revealed movements between islands in N Central Pacific; largely birds before breeding or between cycles. In 1966, 1967, 1968, 60%, 40%, 23.8% of birds ringed as young, sub-adults or adults recaptured elsewhere than island of ringing, but few thought to be breeding when recaptured; many more birds may congregate on an island than ever breed there. But (given fairly high mortality) enough of cohort of year return to natal island to indicate natal philopatry common. Breeding

philopatry almost total, though record of bird breeding on 2 islands in Hawaiian group. Dearth of evidence about fidelity to precise territory and mate. On Tower, several pairs together 2 successive breeding attempts; probably the rule though with exceptions.

AGE OF FIRST BREEDING: 3rd or 4th year (2 or 3 years old), most commonly 3–4 (Johnston Atoll) probably later in some cases. Proportions of age groups (on nest, Johnston 1984–95, possibly breeding 1st time: 2 years 17%, 3 years 32%, 4 years 23%, 5 years 17%, 6 years 8%, 7 years 2%, 8 years 1% (Schreiber *et al.* 1996).

NON-BREEDING YEARS: No firm evidence from marked birds but strong circumstantial, mainly presence of substantial proportion adult plumaged, non-breeding birds in colonies; many ringed on Kure turned up on other islands. Probably spends considerable time wandering.

LONGEVITY AND MORTALITY: known to live 22 years but probably can live much longer. Only data on adult mortality from Woodward (1972) but incomplete. Lowest figure in any one year 7.2% and even this max figure for that year; perhaps some marked birds were missed. 15.3% apparent mortality from sample of 301 birds (1965–66), when adjusted, probably means *c.* 8% mortality. Mortality in first year difficult to estimate. Of 607 chicks ringed, *av c.* 20% sighted following year, but scale of emigration or extended nomadism unknown. On reasonable assumption that most survivors would return to natal colony by 3rd year, 12.9% of 235 nestlings actually seen alive 3 years later represents min figure for survival; probably no more than 75% of 235 nestlings died in those 3 years of which (assuming mortality rate independent of age after year 1) probably 55–60% died in 1st year. In line with equally approx figures for most other boobies.

Masked Booby *Sula dactylatra*

PLATE 5

Sula dactylatra Lesson, 1831, Ascension Island.

Binomial synonyms used in past: *Sula personata*, *S. cyanops*, *S. elegans*, *S. melanops*, *S. nigrodactyla*, *S. bassana*, *Parasula dactylatra*, *Dysporus cyanops*, *Pelecanus piscator* and *P. bassanus*. Wood-Jones (1912) called *S. dactylatra* on Cocos-Keeling *Sula abbotti*. Rothschild and Hartert (1899), Snodgrass and Heller (1904), Gifford (1913), Fisher and Wetmore (1931) used *S. variegata* for Galapagos form of *S. dactylatra*. Rothschild and Wetmore later corrected (Murphy, 1936).

Other common names: white booby, blue-faced booby—both widely used.

French: fou masqué, fou generau. German: maskentöpel. Spanish: piquero emmascarado, piquero blanco, boba de cara azul.

Sub-species

S. d. dactylatra Lesson (Caribbean and Atlantic) smaller than Pacific races; bright orange legs (pre-

breeding males). *S. d. personata* Gould (Central Pacific with W extension). *S. d. melanops* Heughlin (west Indian Ocean). *S. d. bedouti* Mathews (Cocos Keeling, Banda Sea, NW Australia). *S. d. granti* Rothschild (Galapagos; Malpelo—E Pacific). *S. d. californica* Rothschild (Clipperton; W Mexico). *S. d. fullageri* O'Brien and Davies (N Tasman Sea). *Bedouti* said by Mathews to have smaller bill than *personata* and bluer feet but unsubstantiated. Murphy concluded use of soft-part colours to separate *granti* and *californica* unjustified and that sub-specific division within E Pacific not adequately demonstrated. He concluded masked boobies from Revillagigedos, Galapagos, Ecuador, N Peru and Chile should all be *S. d. granti*. May be no justification for more than *S. d. granti* and *S. d. personata* for entire Pacific, even assuming these two usefully separable. Separation of races should not rely on colours of dried soft parts; should take sexual and seasonal variation into account. Pitman and Jehl (1998) conclude, for example, that yellow-billed populations only marginally different from each

other and not separable from yellow-billed form that ranges over most of tropical Pacific—*S. d. personata*. However, yellow-billed forms differ from orange-billed in proportions, plumage, habitat, and distance offshore at which they typically forage. Most importantly, where they nest sympatrically, orange and yellow-billed forms tend to pair assortatively. They thus recommend that *S. d. granti* be recognized as a separate species and named Nazca booby. To me, unnecessary splitting.

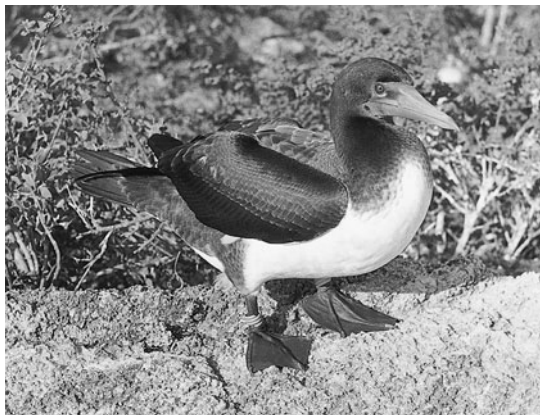
Description

ADULT M PRE-BREEDING: Dazzling white except black primaries, secondaries, humerals, tail. Inner webs of primaries greyish, secondaries white at base. Base, and often centre of tail, white. Black on wings and tail may bleach. Underwing white except for parts of primaries and secondaries not masked by underwing coverts. Dark skin around face (orbital ring, eyelids, facial skin around beak, gular area) contrasts sharply with white head. Bill colour varies with region and season (below). Iris usually yellow; dark brown in Norfolk Island subspecies. Feet from dark grey, sometimes hint of purple, to orangy or drab olive. Ascension, both sexes yellow bills; Los Hermanos, greenish-yellow; Mait Island (West Indian Ocean) orange to yellow; Chagos archipelago (with young) grey-green to yellow; North Cocos of Cocos Keeling yellow, grey-green base; Coral Sea bright yellow (M) dull yellow/green (F); Galapagos orangy (M), pinker (F); Clipperton yellow, tinged pink; La Plata bright orange-yellow at base (M), pink (F).

ADULT F: As M. except (sometimes) soft parts.

POST-NUPTIAL: Little change; soft parts duller.

JUVENILE AND IMMATURE: Crown, forehead, back and sides of neck, nape, ear-coverts mainly or entirely brown, often glossy, sometimes flecked white. Scapulars, wing-coverts warm brown, lighter margins to feathers. Back, rump brown, former pale edges to feathers sometimes giving faintly barred appearance. Primaries, secondaries, tail-feathers dark brown sometimes blackish.



6.73 Newly-fledged juvenile masked booby, Galapagos.

Underparts white extending onto base of neck (sometimes faint collar), up onto throat in inverted V. Brown thigh patch. Underwing mainly white with brown patch. Bill yellow-horn often suffused blue-grey in patches. Facial skin darkens from light blue of chick to blue or blackish. Iris lightens from dark brown of chick to lead grey in juvenile. Legs, feet remain greyish with, in some races, tinge of colour (greenish legs, yellowish webs, in Caribbean). Replacement of juvenile plumage begins 5–7 months; *c.* 2 months after can fly may already be shedding innermost primaries, soon followed by body feathers. Thus in first year may lose juvenile appearance. Head turns first; 9 months slightly speckled brown, 14–15 months pure white. Back, wing-coverts whiter *c.* 7 months, 14 months slightly flecked brown, 17 almost white. Rump brown till 13 months, by 20 months white with few brown specks—last immature plumage to be lost. By 20 months bill dull yellow, facial skin darkening, iris nearly pure yellow, legs, feet dull version adult. Full adult plumage 3–4 months before age 3.

Field characters

Overlaps at sea with all other sulids; scope for confusion. Adult larger, more robust than white morph red-foot; black tail, black humerals, lack of white gap between innermost black secondaries and body diagnostic. Black 'mask', orange-yellow bill distinctive. Australasian gannet yellow-buff head, some

white outer tail feathers, lacks black humerals (as also does African which may have all-black tail). Adult Atlantic lacks black secondaries and humerals, has all-white tail. Juvenile and immature sulids confusing—e.g. adult masked booby confused with late-immature Atlantic gannet, led to records of masked boobies off W Africa and in Biscay. Principal features juvenile masked: large size (useful only against red-foot and male blue-foot), 'V' extension of white onto throat (apex up), distinguishes from adult brown booby and juvenile blue-foot (demarcation line straight across); lacks white rump and nape of juvenile blue-foot. Post-juvenile variable; no simple separation from all possible plumages of others but see other sulid juveniles.

Measurements (see Appendix)

Voice

Noisy. Calls dimorphic. Male whistles thinly, piercing when excited, flute-like when relaxed. Calls single or in small bursts. Advertising whistle descends in pitch 'whee-ee-oo', duration 2–3 sec. Female shouts or honks, variable in pitch and amplitude with short, descending syllables, occasionally fractured. On site, short, soft, talkative notes. Structural differences in syrinx (Murphy 1936). Juveniles have female-type voice which male retains until 3rd year (may have adult plumage and soft parts). Could this prevent breeding attempts before physiologically mature?

Range and status (Figure 5.15)

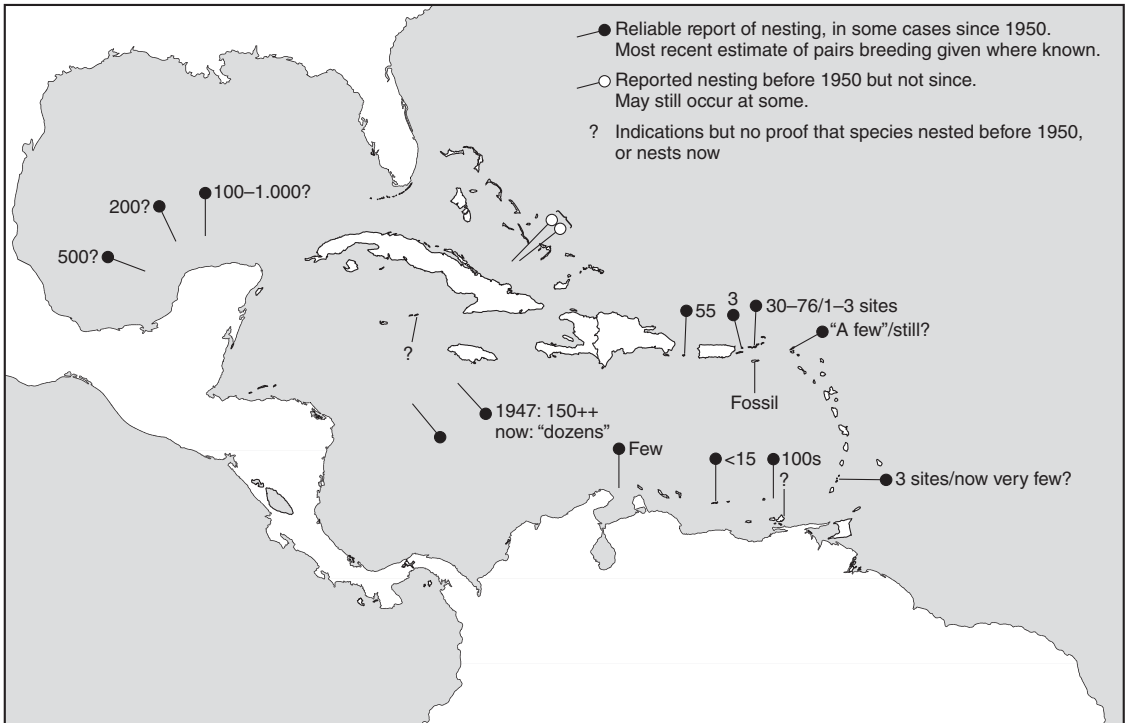
Breeds *c.* 25°N–29°50'S, one of 3 pantropical blue-water boobies (others red-footed and brown), but penetrates S to Lord Howe Island (Tasman Sea). More pelagic than brown, avoiding muddy inshore and estuarine waters. Assessment of world population hindered by wide distribution and many hundreds island groups in Polynesia, Melanesia, Micronesia and Indonesia virtually unknown for seabirds but many now peopled and boobies gone. Used to be abundant in Caribbean but much declined. Scattered thinly over more than 20 colonies in West Indies. Boatswain Bird Island a major South Atlantic colony. Largest (ancient) colony off Brazil (over 200 km) on Rocas Reef (Schulz 1998). First record for Lobos de Tierra

(Peru)—10 pairs (Jahncke and Gova 1997). Widely distributed on Indian Ocean atolls, now no major colonies. Huge distribution over Pacific. Vast number of islands in E and centre mean usually small to moderate colonies, but huge areas with few islands in E Pacific. Malpelo possibly world's 2nd largest colony; 24,034 birds, 1992, aerial photo (Pitman *et al.* 1995). Galapagos still large population, *c.* 2,500 scattered pairs (Tower), several thousand (Hood), huge but unestimated population Wenman (Nelson 1978b). Overlaps with 6 of the 8 sulids (Australasian and African gannets, red-foot, blue-foot, Peruvian and brown boobies) and used to do so with Abbott's. World population not known, but much declined; pessimistically may be fewer than 80,000.

MOVEMENTS: Disperses widely outside breeding season. Extreme vagrancy includes record from Mediterranean. Birds ringed as adults sometimes recovered on non-natal islands possibly suggesting some interchange. Birds ringed as nestlings also recovered on islands far distant from natal one.

Foraging and food

Generally forages within 200 km of land, often closer. Between Tahiti and Kiritimati (Phillips and Wragg 1993) 75% of masked boobies sighted within 50 km of land and furthest *c.* 270 km. Anderson and Ricklefs (1987) radio-tracked breeding masked boobies (Galapagos); most foraged in fairly discrete area no nearer than *c.* 65 km to colony. Some correlation between deduced foraging area and presence of sub-surface banks (water depth 33–179 m). Fished in intensive bouts of 5–20 mins. Feeding triggered by sight of another bird diving and may converge from at least a km forming fishing flock within 1 min. Between times sit on water, sometimes putting head under, possibly looking for prey. Observation that with few exceptions adults returned at night, *contra* Tower (Galapagos) where most returned afternoon (personal observation). Masked boobies often fish singly, or commonly in twos or small groups though bigger flocks seen feeding inshore with brown boobies. Fish opportunistically with other seabirds in association with predatory fish and



6.74 Breeding distribution of the masked booby in the Caribbean (probably <2500 pairs). (From Halewyn and Norton 1984.)

marine mammals such as dolphins. Mills (1998) concludes that presence of pursuit divers in mixed feeding flocks increases time for which flock coheres. In E tropical Pacific, transects (Ballance *et al.* 1997) yielded 407 'booby flocks' (masked and red-footed), discrete (not mixed with petrels, terns, etc.) and in areas of shallowest thermocline and highest chlorophyll content (i.e. high productivity). Nevertheless, solitary offshore or pelagic foraging probably usual.

Cooperative feeding not described, but bugle-like double honk, unlike calls of either sex in colony, has been heard just as dive begins, and apparently elicited approach, even from brown boobies.

Mean (radio-tracked) flight-speed 38.3 kph (Anderson and Ricklefs 1987). Typically flies fairly high with bill pointing down. Before diving often fans tail, feet lowered and spread sideways, wing-tips winnowing. Then gravity-plunges with half

twist, or power-dives with rapid wing-beats. Plunge heavy and steep but lacks verve and swerve of acrobatic blue-foot. Penetration conservatively estimated at 2-3 m but from dive of 10-35 m must often be deeper. D.W. Anderson records hovering at 25-100 m before diving. Can take very large prey, which suggests deep diving. Will take flying-fish on wing. Not known to feed at night. Typical flock-size returning foragers (Tromelin Island) 3-4 birds; 29% single birds (Le Corre and Jouventin 1997a). Only 10.9% flew back at more than 50 m high. Red-footed boobies returned in bigger flocks, higher and later. These anti-frigate traits less developed in masked, which less often sympatric with frigatebirds.

Murphy (1936) correlated masked booby distribution with flying fish *Exocoetus* sp, *Cypselurus* sp which, with squid, are main prey. Other prey in regurgitations: *Mugil* sp, *Regificola grandis*, *Rastralliger kanagurta*, *Ophioblennius webbi*, *Engraulis* sp,

Scomberesox saurus, *Selar crumenophthalmus*, *Fistularia* sp., *Oxyporhamphus micropterus*, *Benthodesmus simonyi*, *Holocentrus ascensionis* and *Centrolophus niger* (e.g. Harrison *et al.* 1984b, 1983; Marchant and Higgins 1990). Like other sulids, takes many small items (av 50 per sample on Ascension) or 1–2 large ones (max 41.3 cm in Kermadecs). Dorward's (1962) sample of 28 regurgitations on Ascension showed 390 of 430 items under 10 cm, 38 15–25 cm. Much overlap in diet of masked and brown boobies. In Somoa Harrison *et al.* (1984b) noted prey items per sample av 3 (1–6), length 74 mm (56–89) $n = 4$. In Hawaii (Harrison *et al.* 1983) fish contributed 97% of prey, squid 3% (cf. 27% in red-foot).

Habitat and breeding biology

(See Fig. at end of ch. 5; Dorward 1962; Nelson 1967b, 1978b; Kepler 1969)

HABITAT: Pelagic booby of tropical oceans, often with widely dispersed and unpredictably scarce prey. Roosts and nests on low, sandy cays, coral beaches, arid volcanic islands either bare or with zerophytic scrub but not usually bird of heavily vegetated habitat nor of cliffs, though can use broad ledges even where mainly uses flat ground. Rarely perches on trees. Prefers territory with vantage points. Will walk on thick scrub and tear some away to make scrape. Used to nest widely dispersed over central plain of Kure but spread of *Verbesina* evidently forced them to nest more densely in remaining clear areas (Kepler 1969).

COLONIES: Occasionally large. Highly gregarious but density variable; usually, well-dispersed, often in groups: Kure 1 pair per 42 m²; Tower (Galapagos) 1 pair per 125 m²; Hood (Galapagos) 1 pair per 84 m²; Christmas Island (PO) at least 92 m between most nests; several km separated sub-colonies; Hasikya (Arabian Sea) 1–2 m between nests; Boatswain Bird Island 1 pair per 3.3 m² (densest recorded colony). Can breed as isolated pair. Except at highest densities uses fraction of area and territories shrink by at least 75% after laying. Nesting habitat usually non-limiting.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Given same partners, almost exactly 12 months between successful clutch and next one. On Kure, of 19 pairs which bred successfully in 1964 and



6.75 Examples of habitat and spacing: A Dispersed flat ground, Tower (Galapagos); B Dense, slope nesting, Bosun Bird (Ascension), (Photo: D.F. Dorward); C Widely dispersed among scrub, Kure (Pacific), (Photo: C.B. Kepler).

reunited in 1965, 73.6% took 50–56 weeks between successive layings, 57% laying within a week of exactly one year (Kepler 1969). Others took 47–62 weeks. Failure partway through a cycle may shorten the interval and change of mate lengthens it. Of 4 Kure pairs which failed in 1964 but reunited in 1965, intervals were 52, 53, 56 and 58 weeks. But on Boatswain Bird some pairs which lost egg or chick took only 6–9 months before next clutch (Dorward 1962)—highly variable intervals (excluding replacement layings) which differ from Kure or Galapagos. Many pairs which laid late and unsuccessfully one calendar year laid much earlier the next. In reputedly a-seasonal environment, may be advantageous to fit more breeding *attempts* into a lifetime. Pre-laying, chick-care and post-breeding attendance are adapted to local conditions. Masked boobies attend breeding colony 33–40 weeks/year: 3–6+ weeks pre-laying, 6 incubation, 23–6 care of young and 3 or more post-breeding. Otherwise may rarely visit, or may roost there (regional variation). Although over entire range may lay in any month, large regional differences. Everywhere lays over several months. In Galapagos laying period varies with island; different islands, and groups on same island, often considerably out of step. Lays in waves, which probably coincide with good feeding (see Nelson 1968). ENSO exerts marked effect. In March 1987, Tower (normally would have had large chicks) only 1% of 400 pairs had nestling; *c.* 90% courting (Anderson 1989b). In S of archipelago not, or less, affected. Large colony on Boatswain Bird loosely seasonal and synchronized but marked subgroup synchrony (Dorward 1962). On Kure, only some years show marked peak of laying (Kepler 1969). In 1964 60% of clutches laid within a month; in other years no clear peak. On Christmas Island (PO) synchrony within group but wide overall scatter (Schreiber and Ashmole 1970).

TERRITORIAL BEHAVIOUR: Post-breeding, may visit colony intermittently. Inspects breeding area by aerial reconnaissance and on foot. Ritualized in-flight signals site-ownership. Males out-post on vantage points in alert position (long-necked and forward-leaning) watching neighbours and vocalizing ‘at’ overflying birds. Neighbours tend to ‘out-post’ simultaneously. Territorial fighting or even



6.76 Ritualised ‘fixed gaze’ between mates; precedes further interaction, often ‘mutual jabbing’.

interlocking of bills, rare. Scale of intensity (high to low) territorial behaviour: wing-flailing, jabbing, aggressive site-ownership display (yes/no headshaking). Wing-flailing, an intention movement of flying towards opponent, incorporates high-intensity jabbing and yes/no headshaking with calling. Ritualized jabbing, with ‘head-twist’, between rivals and mates; loud clash of bills. Boundary jabbing prevents trespass, demarcates precise limits of territory. Conditioned neighbour does not trespass even when owner has withdrawn. In yes/no headshaking bird superimposes violent nods ‘yes’ on slow semi-circle of ‘no’. Face enlarged by ruffing head feathers which high-lights black mask. Bill inclines upwards during ‘yes’ movements. Wings may be held loosely, partly raised or even widely spread. Normally ‘yes’ nods concentrated in mid-point but directed at near rival. At high intensity jabs and wing-flailing interspersed. Male calls ‘whee-o’, female shouts harshly. At low intensity display silent. Fixed stare elicits ‘yes/no headshaking’ from recipient. ‘Yes/no headshaking’ often occurs post-landing. Early morning outbursts conspicuous when birds emerge from vegetation and mount vantage points. Derivation conjectural. Resembles food-begging of young. High-intensity begging in large young includes both ‘yes’ and ‘no’ and wing-flailing and calling. During chick’s development begging grades into ‘yes/no headshaking’;

an intruding adult may elicit begging which slides into this display.

PAIR-INTERACTIONS: Early in season, overflying birds elicit sexual 'advertising' (sky-pointing) from territorial males. Prospecting females land in vicinity and 'peer' in long-necked forward-leaning posture, eliciting further display from male which may attract them to close range and initiate a partnership. Sky-pointing typically performed male to female, not reciprocally or mutually; lengthens neck, points bill 45° upwards, lifts wing tips in swivelling movement and whistles through parted mandibles. Between repetitions 'stares' at female. Seen from front, black mask conspicuous against white face and enhanced by bulge caused by depressing tongue bone (cf. cormorants). One bout may contain >50 individual sky-points but av c. 5, mainly to females some distance away; an attractant rather than close-range display. More than 93% of males advertising to overfliers are bachelors displaying indiscriminately to females and males (isomorphic). During early bonding, males time display to coincide with instant when female looks at them. Intersperse sky-pointing with e.g. touching nest-material or ground, 'staring', head-flinging, or even aggressive territorial display. Late in season, when aggression disinhibited, may attack own or neighbour's chick, mixing this with sky-pointing.

Throughout breeding cycle partners constantly interact. In vigorous mutual jabbing partners rush towards each other and thrust open bill into other's,

but may grow out of tense, formalized bill-touching. Accompanying vocalization indistinguishable from aggressive calling. Difference in form of mutual jabbing between partners and in territorial disputes merely one of degree. Most prolonged and intense between new partners and early in season, when may flare up every few sec for up to 10 min. Male may bite, jab or wing-flail at female if she turns her back. To avoid triggering jabbing, partners stand parallel in strikingly stylized manner; often follows bill-touching or by bill-up-face-away.

Quick, vigorous headshake with bill pointed obliquely upwards is associated with mutual jabbing and yes-no-headshaking. Characteristically occurs in birds moving away from mate. Often briskly 'rattle' partly loosened wings. This flight-preparation behaviour often occurs as low-intensity alarm. Chicks do it long before they can fly. 'Bill-tucking', another probable appeasement posture, frequently used, fleetingly, as bird parades around territory. Frequent reciprocal allo-preening and unilateral allo-preening, usually of male's head by female.

COPULATION: (GFA)

NEST: Symbolic; no structural value. Building ritualized; hundreds of fragments collected from near or far, largely by male. Points it, long-necked, at female. Deposition accompanied by soft, sharp whistle (male) or deep call (female). Pair keep heads down together much longer than needed for positioning the scrap. Bill open longer than necessary for deposition; traces of lateral tremoring and sideways nest-building for working material into position, though movements not now needed. Males place 90% of items in front of female but female places almost all in front of herself. Even in symbolic form, nest-building primarily by female. Often apposing bills triggers mutual jabbing; material dropped, sometimes down partner's throat. Nest-touching occurs as displacement behaviour.

EGG/CLUTCH: Egg 1 larger than egg 2 (ratio of volumes 1.113:1, Anderson 1990a). Measurements: 60.4 (57.4–70.6) × 44.4 (40.6–46.6) n = 12 Boatswain Bird; 68.5 (62.8–73.5) × 46.1 (44.4–47.8) n = 8 Willis Island; 66.5–69 × 43–5 n = 10 North



6.77 Ritualised 'parallel standing' (partners).



6.78 Hostile-looking mutual jabbing (ritualised) between mates.

Keeling; 67 (64.5–70) × 47 (46–49.3) Kermadecs. Weights: (Willis Island) egg 1, 80 g; egg 2, 75; egg 1 or 2, 77.5 (70–85); (Boatswain Bird) egg 1 or 2, 67.5 (52–82.5); (Galapagos) egg 1, 69; egg 2, 70; egg 1 or 2, 68.3 (67–70). Egg \bar{c} . 3.6% female weight. Proportion of two-egg clutches varies with region. Mean clutch-size: Ascension 1.3 $n=96$; Kure 1.9 $n=105$; Kure 1.8 $n=229$; Vostok 1.8 $n=97$; Galapagos 1.6 $n=209$; 1.6 $n=378$ and 1.4 $n=163$. Some figures for 2-egg clutches minima (perhaps incomplete). On Kure (6 consecutive years 1964–69), clutch-size varied from 1.57 (1966—wet, windy and breeding late) to 1.94 (1969) (Woodward 1972). In Galapagos also significant variation in clutch-size; over 3 years, 42.8–65.7% of all clutches consisted of 2 eggs (Anderson 1990a). Interval between eggs 1 and 2, 5.6 days (3–15) $n=85$.

REPLACEMENT LAYING: May occur after loss of eggs or young. On Kure (1965) 9 of 21 failures re-nested, but in 1964 only 2 out of 19. Late failures

less prone to re-lay. Replacement clutches contribute significantly to productivity. On Kure av period loss to re-laying 30 days (17–59) mostly 25–30, though stage at which previous attempt failed varied hugely. Re-laying rarer on Ascension and Galapagos, perhaps reflecting energetic cost of extended site-attendance and incubation in these impoverished areas (cost of egg tiny).

INCUBATION: Attendance at site high prior to egg-laying; male more than female. Eggs retrieved if within bill-reach; will roll in more eggs than can cover. Change-over at any time, mostly evening; usually 3–15 sec after arrival. Incomer calls loudly; usually lands at some distance. Brief mutual jabbing or nothing. Shifts (Galapagos) av 30 hr male $n=68$, 25 female $n=66$. Immediately before hatching reduced to 23 and 21 respectively. In Hawaiian Islands stints only 9.5 hr but on Boatswain Bird 27 hr. Incubation period Kure, egg 1, 43.8 days (40–9) $n=58$; egg 2, 42.8 (38–47) $n=48$. Mean interval between hatching (same clutch) 4.7 days

(2–9) and on Ascension 5 days. In Galapagos hatching a-synchrony over 3 years 5.27 days (Anderson 1990a). Hatching gap same as laying gap (5.6 days); chick 1 considerably more advanced than sibling, which it destroys.

CHICK/BROOD: Hatchling 40–60 g. Skin grey or slightly pink with sparse tracts white down. Bill grey with broad pinkish band on upper mandible. Eyes open on hatching, dark blue-brown; feet grey. Week 2 thin, short down covers back and flanks. Week 3 thinly down-covered with bare patches on head and neck. Gular and facial skin creamy or pinkish; later grey-blue. Week 4 thickly down-covered and looks one-third adult size. Culmen length guide to age (Figure 5.27). End week 6 chick fluffy and large; lacks emergent wing or tail feathers. On Kure, wing feathers erupted *c.* 7 weeks and most show primaries then tail. In Galapagos wing feathers erupt *c.* 8 weeks; not visible on closed wing until *c.* 9 weeks. Black wing and tail feathers become conspicuous by 10 weeks (Kure) and a few days later (Galapagos) scapulars growing, then wing and tail-coverts. At 11 weeks these unite in mid-line and bird properly feathered on back. Down lingers on head, neck, flanks, belly, and lower back and (Galapagos) may be thick until week 13, sometimes clinging till week 16. Bill now yellowish-horn with darker blotches. On Kure clear of down 14–15 weeks. Wing feathers fully grown 16–17 weeks and juvenile can fly. Despite retarded development, Galapagos juveniles fly as soon as those from Kure, their wings growing as rapidly though weight lags. Fledged juveniles distinguishable by clean feet. A chick compelled, by manipulation, to share parental feeds with a sibling (which, nevertheless it eventually killed) took at least 3 weeks more than normal to fledge (personal observation).

At 12 weeks, max weight on Kure 2,900 g but in Galapagos only 1,900 g, near Kure minimum. At any given age, anywhere, weight varies enormously. Ability to withstand prolonged starvation, by arresting growth and utilizing tissues, is of great survival value. Kure birds reached a mean max weight of *c.* 114% mean adult weight at *c.* 80 days whereas Galapagos birds did not exceed adult

weight, though in both localities juveniles fledged at approx adult weight. After fledging, weight of birds dropped sharply (cost of flight and missed feeds) before slowly rising as juveniles began to fish for themselves. Growth strongly allometric. Tarsus and middle toe reach adult dimensions at 45 days, culmen at 70–80, primaries and tail about 120 (flight starts 115–24). Rapid growth of feet may relate to need for thermo-regulation when adults stop shading chicks at *c.* 5 weeks. Wing-growth consumes much energy and is of no advantage until late in growth. Whereas weight and culmen grow faster on Kure than Galapagos or Ascension, wings grow fastest on Ascension. Thus, despite substantially slower growth by weight, Ascension birds fledge as soon, or sooner. Not only are wings longer, age for age, up to at least 100 days, but weights are lower. Thus fledglings may begin to contribute to their own keep sooner, in the poorer environment.

Masked extreme case of brood reduction; virtually never rears two chicks, and ‘insurance policy’ remains most convincing interpretation of adaptive value of two-egg clutch. Siblicide achieves optimal brood size. Anderson (1990a) showed that egg 2 contributed the surviving hatchling in 19.2% of 102 two-egg clutches that produced a chick, and had insurance value in all 3 years. The surviving hatchling came from egg 2 after egg 1 failed, in 23% of clutches (1984), 7% (1985) and 25% (1986). Of 7 hatchlings from 2nd egg 5 still alive at 60 days and likely to fledge. The thesis that a brood-size of 1 is not optimal for this booby is invalid.

CARE OF YOUNG: Attendance spells (Galapagos) during first 2 weeks significantly shorter than during incubation: 18 hours (both sexes) week 1; 20 male, 14 female weeks 2 and 3; 18 and 20 weeks 4 and 5; 17 and 9 weeks 6 and 7; 15 and 10 weeks 8 and 9; 14 and 12 thereafter. Duration of brooding and chick-guarding varies with locality; longest early in season. On Ascension brooding stints av 11.6 hr *n* = 20, some change-overs at night. Attacks on unguarded small young by non-breeding adults may cause death. Galapagos chicks first unattended 22–62 days; Kure 29–84. Young fed *c.* 1.4 times

per day (Galapagos). Anderson and Ricklefs (1992) found 78% of weight gains due to recent feeding occurred 14.00–22.00 hr, especially shortly before and after dark. Large young discomfit adult; may take fewer than 20 sec to feed it and depart. On Ascension adults delivered <2 feeds per day (one feed may be several regurgitations), in Galapagos 1.4 per day. At 4 nests watched for 48 hr excluding darkness, males provided 7 feeds, females 4. Parents cannot achieve optimally adaptive chick-feeding since their combined pay-loads may exceed chick's ingestive capacity. A small, starving chick cannot accept feeds from both parents close together. Large chicks can ingest >750 g in one day.

BEHAVIOUR OF YOUNG: Food-begging at first weak and uncoordinated. Later, high-intensity begging is with head laid back, bill pointing up and rapid side-to-side movements whilst nodding up and down and bobbing and feinting with bill pointing down. Wings thrashed violently and vigorous lunges aimed halfway down parent's bill or near base. Calls rapidly, 'aa-aa-aa'. Hungry, unattended chicks may beg for long periods completely *in vacuo*. Seeks shade from *c.* 3 weeks. Hides bill in response to alarming stimuli, even before contact, appeasing intruders, own parent or larger chick. Bill-hiding grades into bill-tucking once begins to move around territory—even when alone. From *c.* 4 weeks performs aggressive 'yes-no-headshake' to intruders, reverting to bill-hiding if attacked. From 8 weeks defends territory with jabbing and wing-flailing. From 12 weeks invariably dispels adult intruders. Full sexual advertising may be shown to both males and females from *c.* 5 weeks accompanied by a 'cow-call' version of male's whistle (sex-linked differentiation of syrinx not yet occurred). After first flight performs pre-landing calling followed by post-landing touching of nest-material and site-ownership display. Hostile jabbing is 'straight'—lacking the flinging movement with open mandibles used in mutual jabbing between mates. May redirect attack (stabbing and biting) to ground or parent.

FLEDGING: First flight(s) brief. First landing on sea feet-first but by second day (perhaps earlier) executes

shallow dives. Boisterous and clumsy, chasing each other and other species with shouts and diving fussily. After beginning to fly revert to precise site of parents, from which wandered during development. Fledging period Kure 117.6 (115–124) *n* = 5; Galapagos *c.* 120 days.

POST-FLEDGING: Free-flying juvenile fed in adult's territory variable period. Galapagos minima: 30, 33, 49, 50, 59, 62 days. Roughly comparable elsewhere. Disappears abruptly to become nomadic.

BREEDING SUCCESS: Hatched from laid: 59.6% (egg 1), 55.1% (egg 2), 76.4% (overall, Kure, Woodward 1972); 48.1% (*n* = 497, significant variation between years, Galapagos, Anderson 1990a); 79.6% (overall, Galapagos, 1964, Nelson 1978b), no significant difference between eggs 1 and 2, 1-egg clutches lower success 45.7% (27–63) than 2-egg—52.6% (38–68). Fledged from hatched: 79.5% (group 1), 25% (group 2), reasons for difference unknown (Galapagos); 25% (*n* = 272, including those from egg 2, Ascension, Dorward 1962). As proportion of *nests* which fledge a chick 79% (1964), 83% (1965, Kure). Fledged from clutches laid: 9.7% (1958, Ascension); 63% (1964, Galapagos); 71.5, 68.3, 69.2, 69.6, 57.4, 86.4% (1964–69, av 55 nests per year, Kure). Egg 2 gave significant proportion of fledglings in 2-egg clutches. Although av survival time of chick from egg 2 only 3.5 days (range 1–15), over 3 years, 68% of 103 2-egg clutches produced a fledgling against 31.8% of 22 1-egg (Kure). Second egg contributed because: first chick died before second hatched; egg 1 cracked or lost. Over 3 years egg 2 produced 13 young and egg 1 60 young. Kepler, on Kure, found that egg 2 produced fledglings because egg 1 failed (10 cases) or chick 1 died early (3 cases). Given clear advantage of 2-egg clutches it may be that 1-egg clutches are largely from young (or very old?) females. Replacement clutches significantly productive. On Kure in 1965 (an adverse year) 6 young (24% of young of the year) came from re-lays. In that year, re-laying more successful than first laying (67% versus 48%) though following year it did not produce any fledglings. Egg failure due to infertility or desertion due to unfavourable conditions. If

eggs properly attended, predation marginal. Loss of chicks usually due to starvation but unpredictable timing of shortages obviates seasonal correlation. Early birds may do well one year, badly another. But in some areas broadly seasonal laying probably advantageous in long term. On Ascension, young most vulnerable at 3–4 weeks—period of max growth and (because unattended) thermal stress. Temporary food shortage can cause adults to leave chicks prematurely, leading to dehydration and death. On Kure, nothing comparable to starvation on Ascension.

FIDELITY TO COLONY, SITE, AND MATE: Breeding philopatry strong but not absolute. 4 breeding birds changed islands in Swain Reef Complex (Great Barrier Reef) (O'Neill *et al.* 1996), at max distance apart of 27.3 km. Kepler (Kure) found virtually no interchange between two discrete groups though less than 90 m apart, separated by belt of *Scaevola*. On Tower, Galapagos, all birds individually marked in Jan back in original areas in Nov (personal observation). Natal philopatry probably weaker. 9 birds captured breeding on non-natal island, max distance from birthplace 123.6 km. Although not nesting, 37 birds recaptured on islands within Swain Reef different from one on which marked as chicks, max distance 127.6 km. Several records of birds moving between islands in Central Pacific—e.g. reared Kure, breeding Midway (POBSP).

Masked boobies return to same colony for each breeding attempt, but not always to precise breeding site. Of 22 pairs persisting for 2 successive years only 2 re-nested within 6 m of old site (mean movement 19.8 m, max 65 m). Movement even greater when partners, though experienced, new to each other. 90% of study population moved from territory of previous year (Kepler 1969). May not be typical. On Tower, of 22 pairs marked 1963–64 and seen late 1964, 8 returned to same territory and further 9 males and 2 females, though alone, seen on their old sites. Thus in 86% of cases one or both pair-members site-faithful. Mate-fidelity moderately strong. Of the 22 Galapagos pairs, 8 intact late 1964 and 11 birds alone on old sites. Thus mate fidelity could have been 86% or only 36%. On Kure, of 42 pairs

which attempted to breed in 1964, 23 remained together in 1965 and 19 split up. Of these 42 pairs, 32 successful in 1964 but nevertheless 13 split up following year. Breeding success only moderately related to fidelity.

AGE OF FIRST BREEDING: May breed first in 3rd year, more usually 4th, sometimes 5th or later. On Great Barrier Reef age at first known breeding (not necessarily first breeding) 3 years (1), 4 (3), 5 (6), 6 (10), 7 (11), and 8 (1) (O'Neill *et al.* 1996)—considerably longer pre-breeding period than hitherto known though infrequent (6-monthly) observer visits would allow undetected breeding attempts. In Galapagos adults feeding young maintained or increased their weight (Nelson 1967b), suggesting lack of stress—possible strategem for increasing lifetime productivity at cost, in some years, of under-provisioning young.

NON-BREEDING YEARS: Of 75 pairs marked whilst breeding (Ascension) only 35 known to attempt breeding in following season though most others seen in colony, including birds successful in previous effort (Dorward 1962). By contrast, on Kure 1965, no unemployed birds. However, 84 birds bred both 1967 and 1968 but 11 bred only 1967 though present 1968. 86 bred 1968 and 1969 but 9 only 1968 (Woodward 1972). On Great Barrier Reef indications that some birds missed breeding years (O'Neill *et al.* 1996) and this seems normal in masked booby. Woodward (1972) demonstrated that on Kure in 1968, 90 of 118 birds in colony were known to have bred previously, 17 were first-time breeders and 11 non-breeders. In 1969 these figures 94, 9 and 9. Thus *c.* 11% of population first-time breeders, 9% non-breeders, leaving 80% of colony composed of experienced breeders. A few birds 2 years old.

LONGEVITY AND MORTALITY: Woodward (1972) demonstrates max av annual adult mortality of 8.6% but 5–7% probably nearer mark. Av life-expectancy probably 16–20 years. During first two years of life max av mortality 67.5% calculated from 206 ringed chicks over 6 years but usual caveats pertain.

Blue-footed Booby *Sula nebouxii*

PLATE 5

Sula nebouxii Milne Edwards, 1882, Pacific coast of America.

Original specimen obtained by Neboux during voyage of Venus in 1839 had no exact locality; Milne-Edwards surmised Chile. Now rare, if at all, in Chile but political boundaries changed. Various referred to as *S. leucogaster*, *S. brewsteri*, *S. cyanops* and *Dysporus leucogaster*. Confusion, since *S. leucogaster* brown booby, *S. cyanops* is one name of masked.

Other common names: camanay (Peru, Chile), piquero (Ecuador, N Peru), bobo de patas azules (Mexico).

French: fou à pieds bleus. German: blaufustolpel. Spanish: piquero camanay.

Sub-species

S. n. nebouxii of California and west South America distinguished from *S. n. exilis* (Todd) of Galapagos. Differences slighter than in sub-species of red-footed and brown boobies and, probably, blue-foot more recently a single population as present distribution indicates.

Description

ADULT M PRE-BREEDING: Head, neck densely streaked, feathers light-tipped, often abraded and apparently split-ended giving spiky, 'chrysanthemum' appearance. End on lower throat in broadly inverted V. Upper breast, rest of underparts white; under wing-coverts grey-brown. Wings deep, burnt brown, usually plain but with grey-brown bloom when new. Scapulars have broad, pale tips giving barred appearance. Upper wing-coverts, back fuscous. Tail feathers mainly darkish brown variably bleached, central ones especially pale; all whitish on basal third. Tail-coverts dark though conspicuous, irregular white rump patch very obvious in flight; another patch at base of neck. Brown patch with white flecks starts above thigh,

extends to base of tail. Bill dark, slate-blue with paler streaks; gular skin similar, merges into bill. Orbital ring slightly darker. Iris piercing yellow, enclosing small, dark pupil. Legs, webs brilliant turquoise or blue, from ultra-marine to lighter.

ADULT F: Larger than male, 32% heavier; proportionately shorter tail. Plumage similar. Pupil surrounded by brown pigment intruding, star-like, into yellow iris.

POST-NUPTIAL: Little change.

JUVENILE AND IMMATURE: Head, neck, throat, upper breast deep brown, almost blackish; browner and glossier after fledging. Sharp demarcation between upper and lower breast; belly, flanks white. Brown of posterior abdomen begins in line with trailing edge of extended wings. Under tail-coverts brown, underwing silver-grey on primaries, paler in area of axillaries and under-wing-coverts. Wings, back deepish brown. Variably sized whitish patch at junction of neck and back; another on rump. Tail brown/black. Bill almost black; after fledging horn or yellowish at tip and feet become lavender, then faint blue or purple. Eyes brown, or more greyish. Immature stages poorly documented. Feathers of head, neck, scapulars, acquire pale or buff tips, eye lightens, bill turns bluish from tip. Feet light grey-blue gradually deepening and brightening. Even after head streaked birds may retain traces of dark on upper breast down to pectoral band; may breed in this condition.

Field characters

Spiky, streaked head diagnostic. General demeanour shag-like; highly mobile on ground and acrobatic in air. Spare and rather upright, with cocked tail and sinuous neck. Juvenile: marked demarcation line between lower breast and abdomen; conspicuous white nape and rump patch. None of these occurs in juvenile brown, masked, or Peruvian, which may breed in same locality.

Measurements (see Appendix)

Male smaller than female and proportions differ. Significant regional differences (Galapagos largest). Female is *c.* 32% heavier than male but his tail is almost as long, thus longer than hers in proportion to body and wing-length. His bill, shorter in absolute terms, is longer in proportion to body weight; hers disproportionately more powerful. Physical differences must predispose to different feeding niches. (See Guerra and Drummond 1995 rereversed sexual dimorphism; Torres and Drummond 1997a re female young suffering higher mortality than male.)

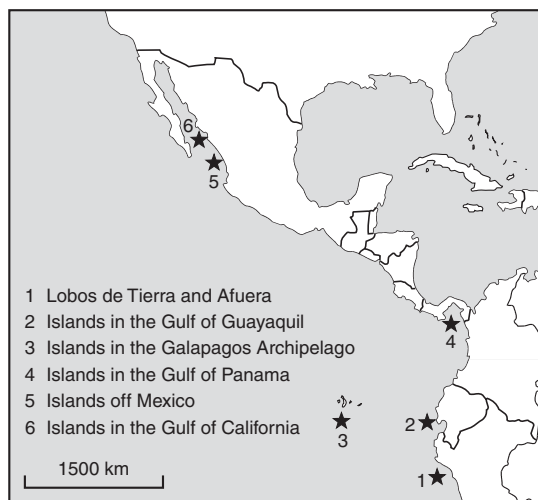
Voice

Male's light, throaty whistle ranges from husky through sibilant to piercing; 3–4 in quick succession 'phew-phew-phew'. Advertising call, single, drawn-out whistle gradually fading. Female shouts or grunts with deep, pleasant timbre 'ark-ark-ark'; groans when advertising. Differences correlate with structural differences in syrinx (Murphy 1936). Speed and quality of syllables varies giving conversational effect during pair interactions. Many pairs 'talking' give impression of considerable social stimulus within group, which breeds synchronously. Aggressive call of chick 'aa-aa-AAH-ah'. Food-begging juveniles emit 9 'cacks' per cackle-bout when pestering adult. High-pitched 'yip' common to tiny sulids deepens into female-type voice. Age of voice-change in male not recorded. Vocalizes during communal fishing.

Range and status (Figure 5.14; 6.79; 6.80)

Rarest booby after Abbott's. Limited range compared with three pan-tropical boobies may relate to more specialized requirements. Essentially bird of fringe of E Pacific cold-water upwellings; confined to zone between S California and N Peru currents.

Highly discontinuous along *c.* 3000 km of coastline between Lobos Islands of Peru and Gulf of Panama. Lobos de Tierra and Lobos de Afuera (S limit breeding range) long-established, major Peruvian colonies though blue-foot seen as far S as Pisco and, during climatic upheavals, even Chinchas. At latitude of Lobos Islands anchovy already thinning out but abundant enough to



6.79 Broad features of the breeding distribution of the blue-footed booby. (From Nelson 1978b.)

sustain large numbers of blue-feet whereas further S, where anchovies at max density, Peruvian booby may exclude them. Blue-foot nested all over Lobos de Tierra in 1963 (possibly 10,000 pairs) though big decrease from 1920–50 (Tovar 1968).

Important outpost in Galapagos—*c.* 10,000 pairs, perhaps 6th of world population. Largely confined to islands S of equator; nearer to Humboldt current, which swings NW from coastal Peru. Some 34 'colonies' (ill defined); important ones on Daphne Major, and Hood.

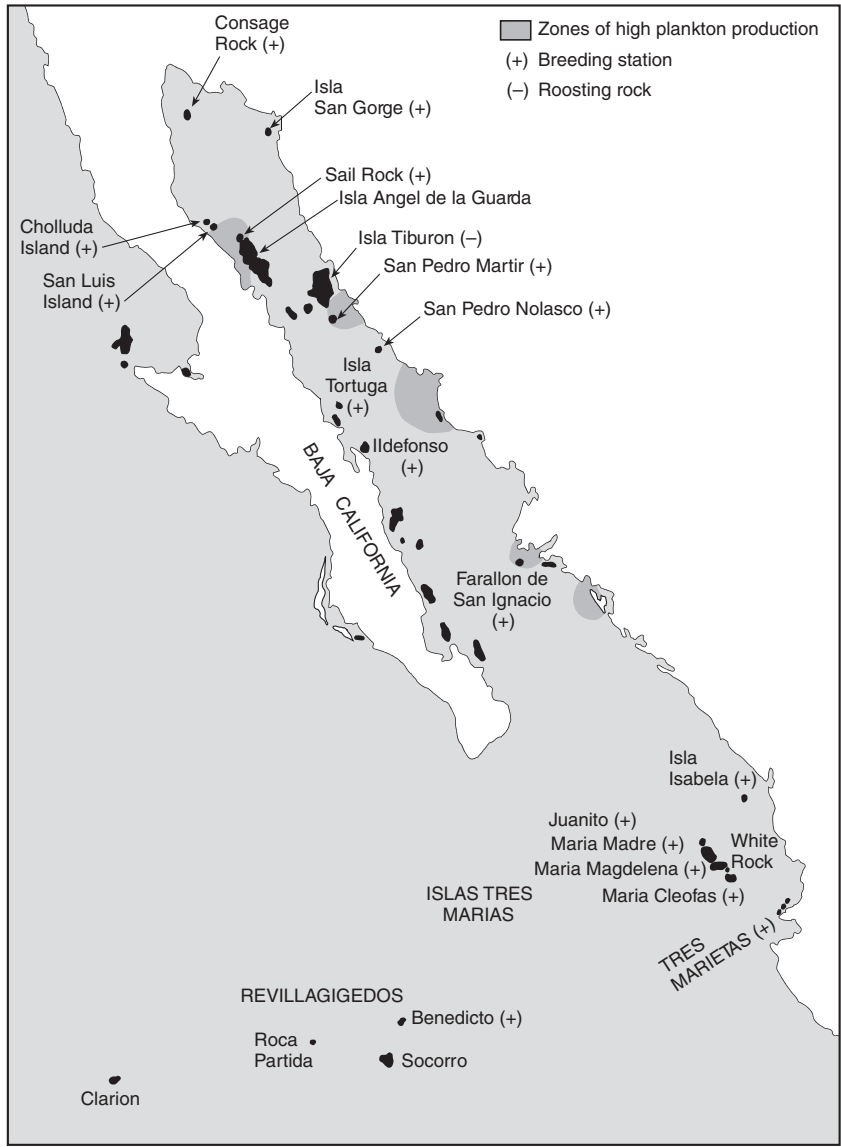
May be substantial numbers in Gulf of Guayaquil especially on El Muerto where formerly abundant. Reputedly breeds on islands in La Plata area (no details). Then comes coastline of 1000 km before Gulf of Panama. Around Pearl Islands especially abundant on Galera and rocky island of Camote (Robbins 1958); most numerous booby along coast from Carachine Point to Pinas Bay.

Off Mexico breeds on: Revillagigedos; status on San Benedicto, which formerly held hundreds of pairs, obscure. Tres Marias; has long nested on Juanito, Madre, Magdalena, White Rock, and Cleofas. Reasonably recently Juanito and Cleofas still retained colonies but Madre and Magdalena not mentioned in Grant and Cowan (1964) or Stager (1975). Isla Isabel(a), 35 km due W of Nayarit, an

ancient colony (now a reserve), held ‘many hundreds, possibly a few thousand, at various stages of breeding’ (Howell 1975) but present population probably 1,000–2,000 pairs (Drummond personal communication). Tres Marietas; two large islands, one small and some rocks, 4–6 km offshore. Largest held *c.* 1,500 birds (May 1961), 1,100 (May 1962)

and 750 (April 1963) (Grant and Cowan 1964). Perhaps reduced but amount of disturbance unclear (Drummond personal communication). Also breeds Gulf of Fonseca.

Seabirds of Gulf of California probably once rivalled those of Peruvian islands; fraction remains. Cool Californian Current flows S between 48° N



6.80 Breeding stations of the blue-footed booby in the Gulf of California and off Mexico, and major plankton-producing areas. (From Nelson 1978b.)

and 23°01'N along coast of western North America. During spring and early summer it is N hemisphere equivalent of Humboldt with upwelling cold water and areas of rich primary productivity supporting many fish. At least 10 islands known or suspected to hold blue-footed boobies; may total 85,000 birds—diminishing because grossly disturbed (D.W. Anderson—summarized Figure 6.80).

World population perhaps: *c.* 10,000 pairs Galapagos, probably tens of thousands of birds Gulf California and Mexico, probably far fewer than 100,000 birds Peru. Unknown number W coast South America.

MOVEMENTS: Notably sedentary around breeding area. Galapagos birds move as far as coast of Ecuador. Juvenile dispersal usually less than 500 km. Failure of food may stimulate more extensive dispersal, including adults, >1000 km.

Foraging and food

Feeds close inshore, even inter-tidally, and offshore to at least 30 km, probably much further. Flight speed *c.* 39 kph (Anderson and Ricklefs 1987, 1992). Notable sexual dimorphism suggests significant differences in foraging, feeding, and target payloads. Small, light, long-tailed male sometimes dives close inshore in as little as 15 cm of water, which heavy female could not do. Her large body-size and extremely long bill enable her to catch large prey and/or carry heavy payloads which male could not (see Anderson and Ricklefs 1992). But Guerra and Drummond (1995), based on regurgitates, found little size difference. Even if sexual dimorphism arose primarily under selection pressures other than feeding (such as courtship), it would be expected to impinge on feeding.

On Hood (Galapagos) female's outward-bound foraging lasted 2–3 times longer than inbound (cf. masked in which journeys about equal) suggesting that blue-foot searches rather than travelling to predetermined area, though typically did tend to fly in certain direction (30–165°, mainly 50–105°) (Anderson and Ricklefs 1987). But same individual flew on several different bearings. Of 20 females tracked, 15

absences <2 hours, longest 6.6. Mostly returned at night. A dawn–dusk 9-day survey at sea to W of Galapagos noted blue-feet feeding with other seabirds, sometimes in 'frenzies' and with more than 1,000 boobies involved (Merlen 1995). Boobies followed dolphins, who located shoal and drove it near surface at which point boobies began diving. Frigatebirds which had been maintaining station at height then forced boobies to disgorge (waved albatrosses often then moved in to snatch regurgitate). Feeding associations moved at considerable speed, sometimes for hours. Areas not usually predictable. Thus tendency to disperse widely and join feeding group opportunistically is adaptive.

Diving described by Delano (1817) *c.* 200 years ago 'These birds collect together in small flocks for the purpose of diving. They fly round in a circle and continue to rise till they get to the height of from 60–100 yards... when one of them makes a pitch to dive, at which motion everyone follows. They fly down with remarkable swiftness till within 4 or 5 yards of the surface and then suddenly clasp their wings together and go into the water with the greatest velocity that can be conceived of... with such force as to form a curve of 30–40 yards... before coming to the top again, going to a great depth under water'. Drummond has never seen a dive from higher than *c.* 30 m. Essential refinement in blue-foot is coordinating whistle of a male (female not recorded in this role). Parkin *et al.* (1970) describe small groups (2–13) of birds (both sexes) working a small area, flying 5–30 m above sea and some or all diving simultaneously but silently immediately after one had whistled and dived (see also Atlantic gannet). Drummond has never seen or heard anything to suggest coordination. Local differences? Blue-feet often dive long and slanting, from modest height, but also make impressive, straight plunges. Harris (1974) records power-diving at about 10° to horizontal. Often birds hardly break flight but slice through the waves. May dive from surface and emerge with fish. One male submerged on spot with sharply inclined head and neck and high, vigorous wing-flip. It sometimes moved over surface with lifted wings and jumped

almost clear rather like a shag, before diving (personal observation). Juveniles may dive from surface, swimming quickly along with head under. This technique, followed by small dives from low height, may be common stage in sulids during acquisition of full dive.

Hood birds preyed largely on sardines *Sardinops sagax*; this genus important prey in Gulf of California. Anchovies principal food in Humboldt environs. Flying fish *Exocoetus* sp and squid significant; mackerel *Scomber japonicus* taken. In Galapagos in 1986–87 ENSO caused greater decline in *Sardinops* than in *Exocoetus* which may explain why blue-foot suffered whilst some populations of pelagic masked booby did not (Anderson 1989b). Mexico, 1992, ENSO caused complete failure (Wingfield *et al.* 1999).

Habitat and breeding biology

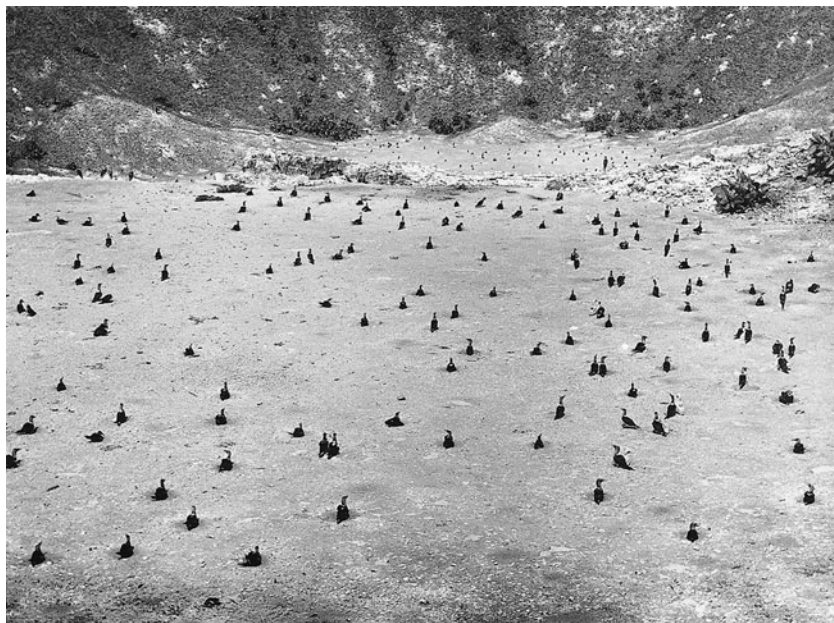
(See Fig. at end of ch. 5; Nelson 1978a, 1978b; Drummond personal communication and public cited, for Mexico)

HABITAT: Fringes of cool water, preferring exposed, often arid islands, though tolerating range

of terrain, vegetation, and climate. Accepts degree of insolation and heat perhaps greater than any other sulid, as in 'baking and insufferable crater' of Daphne Major (Galapagos). Seems ill-adapted to wet, heavily vegetated islands and prone to entanglement. Although uses slopes, and will roost on cliff ledges, unusual to nest there.

COLONIES: Typically contain scores or hundreds rather than thousands. Nests generally well dispersed and, in irregular terrain, prone to clumping. On Isabel mean nest density 0.36 per m² (Osorio-Beristain and Drummond 1993) whilst in Daphne's crater, flat and uniform habitat, c. 0.5 pairs per m². But av densities mean little; nests can be 1 m apart, centre to centre, or separated by 10–20+ m. Will nest solitarily. Above authors calculated that male or female breeding for first time had, within likely settling radius from birthplace, c. 60–90 other nesting pairs. Well-spaced nesting correlates with its highly ritualized locomotory displays.

FREQUENCY, TIMING, AND DURATION OF BREEDING: On Hood one female laid 4 times, each 40 weeks apart, another laid 2 clutches 33 weeks apart



6.81 Bare, flat nesting habitat and spacing in blue-foot (crater bottom, Daphne, Galapagos).

(Nelson 1978b: 544–5). Breeding frequency of 2 males *c.* 35 weeks though not known if same female each time. Together with less complete records these suggest an 8–10-month (probably *c.* 9-month) breeding frequency on Hood. Accords with bluefoot's rapid chick-growth and reduced period of post-fledging feeding. Possible that male breeds more often than female by abandoning a cycle partway and pairing with new female; males with part-grown young advertised from a 2nd site at considerable distance. Loss of egg or small chick can be followed by new attempt within 3 weeks (egg-loss), *c.* 4 weeks (chick-loss) if conditions favourable. Otherwise abandon colony.

Extended-season or (some populations) non-seasonal. In Galapagos may lay in any month though islands differ in month(s) most favoured for beginning a cycle. Large colonies may give impression of non-stop breeding activity but small ones may temporarily be wholly deserted. Even large colonies do not sustain steady level of breeding activity—for example, comparatively few eggs on Daphne July–Sep. Feb–May favoured for initiation of clutches on some Galapagos Islands, Jun–Aug peak on others. During food shortages may suspend breeding, desert, or fail, possibly shortly to be followed by upturn in breeding. Anderson (1989b) found blue-feet most affected of 3 booby species in Galapagos by 1986–87 ENSO. Reflects preference for fringes of cold upwellings, which are affected by such perturbations. Most chicks died and breeding areas deserted (mass invasion of mosquitoes may have played a part). Effects especially conspicuous on Punta Cevallos (Hood) where chicks of masked boobies thriving whilst those of blue-feet dead or dying (different foraging regimes). Similarly, in 1992, ENSO caused complete reproductive failure on Isabel (Wingfield *et al.* 1999).

Over long span, laying in Galapagos may be most concentrated April–May and Oct–Nov but 9–10-month cycle (Nelson 1978b) brings succession of pairs into breeding condition throughout year and these await favourable external conditions before laying. Elsewhere regimes different. On Tres Marietas and Tres Marias Jan–Mar seems main laying period but with large spread; on Isabel mid-Dec–late July with Jan–March peak; rich upwellings of Californian Current in spring–early summer,

reduced in late summer. But this climatic system not invariable, which may favour considerable spread. Within Gulf, Feb–March again seems favoured laying period, with large spread. Here, breeding cycle may be annual, though not demonstrated. No recent information on laying regime on Lobos Islands of Peru. Coker (1920) said breeding appeared continuous but this need not mean equally spread.

Loose synchronization within major groups, such as each of two craters on Daphne, but differences in timing between groups. Synchronization within small sub-groups even more marked. But wide spread of laying and likelihood of 2–3 waves in any one year also important. Spread results not from few pairs laying outside main, well-defined peak period, but from sub-groups, each well synchronized but laying sequentially. Overall synchrony and sub-group synchrony confer different advantages, former largely to do with food, latter with social factors.

Apparent non-breeders within colony but no details on numbers or status.

TERRITORIAL BEHAVIOUR: During pre-laying (Hood) male present 40% of 180 checks, 18% female; Isabel little difference (Osorio-Beristain and Drummond 1998). Pair may divide time between 2, 3 or 4 territories separated by up to 50 m, occupying all within space of an hour (Hood). Site-establishment preceded by aerial reconnaissance (ordinary flight) then display and ritualized territorial circuiting. Reconnaissance may involve group (12–15) which, by settling in same locality, could breed synchronously. Territorial circuiting—rapid flights around breeding area (typically 15–30 sec)—ends in ritualized landing. In-flying male whistles loudly and before touch-down throws up webs which flash against white belly and holds them so until last instant. This 'saluting' ceases after laying. After 'salute', landing male goes straight into site-ownership display (below) and handles nest-material. Overt fighting rare. Other aggressive site-ownership behaviour: wing-flailing, jabbing, threat-gaping and complex display 'yes head-shaking'. Wing-flailing, at territorial boundaries, close-range, expressing tendency to fly at opponent. On upstroke of flailing, male whistles (female grunts) and darts bill forwards.



6.82 Mutual sky-pointing (sexual advertising and pair bonding) display. Note that they already have one egg (clutch normally 2).

These may follow 2 or 3 shallow downstrokes during which moves towards rival, whistle becoming prolonged or grunt rising to crescendo. Withdrawal incorporates bill-hiding, marked in lone birds facing a pair. Jabs rapidly and vigorously, often with head-turn. Vocalizes and ruffs head feathers. Site-ownership display vigorous up-down nodding of head (hence 'yes-head-shaking') so rapid that head and neck vibrate and movement a blur. No obvious side-to-side movement (*contra* masked booby). Usually accompanied by 3–4 syllables. At high intensity accompanied by jabbing, wing-flailing and handling nest-material. Commoner in male, typically as early-season post-landing behaviour and response to intrusion but not uncommon in pair-interactions. Part of prolonged behavioural mosaic as pair parade around, take-off, fly round, land and court.

Probably derives from redirected aggression, touching, or biting ground. When 'yes-headshakes' holding nest-material, often superimposes nodding onto high, arcing movement by which it 'shows' nest-material.

PAIR INTERACTIONS: Prospecting females locate potential mates by aerial inspection of colony; site-occupying males may 'sky-point' (sexual advertising and pair-bonding display). Both in its form—extreme spreading and rotation of wings—and by sky-pointing to each other simultaneously, blue-foot's display represents extreme within family (Figure 6.82). Skyward pointing of bill, elevation of tail and busking of wings accompanied by wing-rotation and spreading, now so exaggerated that dorsal surfaces face partner. Display accompanied by whistle (male), grunt (female). Closely resembles homologous display of cormorants, again suggesting particularly close relationship to ancestral cormorant–sulid stock. Males use it to initiate pair contact, to attract female to nest-site, as prelude to copulation and as pair-bonding—more rarely 'against' overflying males, presumably territorial. Females may sky-point persistently and unilaterally prior to copulation. In early stages of relationship pair repeatedly take-off, fly round in tandem (male leading), and land with calling and foot 'salute'. May then 'parade' around territory with bill tucked, frequently alternating this with curious head position, bill pointing up and head turned to one side. In this 'bill-up-face-away' they briskly shake head—*c.* 3 stereotyped flicks. During parading, which may be 'on-the-spot', brilliant webs spread and lifted ostentatiously. Picking up scrap of nest-material induces intense parading and 'showing' of item. Parading closely linked to precursor of flight—brisk 'rattle' of loosened wings. Early in cycle almost all movement in this exaggerated mode greatly increasing visual impact of all activities which involve locomotion.

COPULATION: (GFA)

NEST: Mere scrape, perhaps between or alongside a boulder, beneath scrub or completely exposed. Within territory pair may hold two or more sites before egg-laying. Thin ring of guano may surround site but no material of significance.

Although no structure, ritualized fetching, showing and 'building' scraps of material presumably reinforce pair-bond.

EGG/CLUTCH: $62.21 \pm 2.66 \times 41.86 \pm 1.7$ $n = 19$;
 62.7 (57.8–69) \times 42.5 (38.8–48.0) $n = 62$; 59.6



6.83 Symbolic nest, among boulders, Hood, Galapagos. Note sex difference in size of pupils.

(57.3–62.6) \times 41.8 (40.5–43.0) Gulf of California. Weight: egg 1 65.4 (54–82) $n=25$; egg 2 64.0 (53–76) $n=14$ Hood; 53.8 (47.9–59.0) $n=10$ Gulf of California. Clutch 1–3, usually 2, very rarely 4 (2 females?). On Hood 85% of 182 clutches followed to completion held 2 eggs, 12% 1 egg, 3% 3 eggs. On Lobos de Tierra 47.35% 2 eggs, 32.3% 3 eggs, 20.4% 1 egg (Coker 1920); proportionately more clutches of 3 than on Hood. Mean clutch-size, Hood 1.9; Lobos de Tierra 2.1+. On Tres Marietas about equal numbers of 2 and 3 eggs (large sample). Incomplete records for Gulf of California indicate av 2.1. Clutch of two $c.$ 7.2% female's weight. Eggs laid mean 5.02 days apart (4–6) $n=13$; hatch 4 days apart.

REPLACEMENT LAYING: A lost clutch replaced in 24 days (Hood, marked birds).

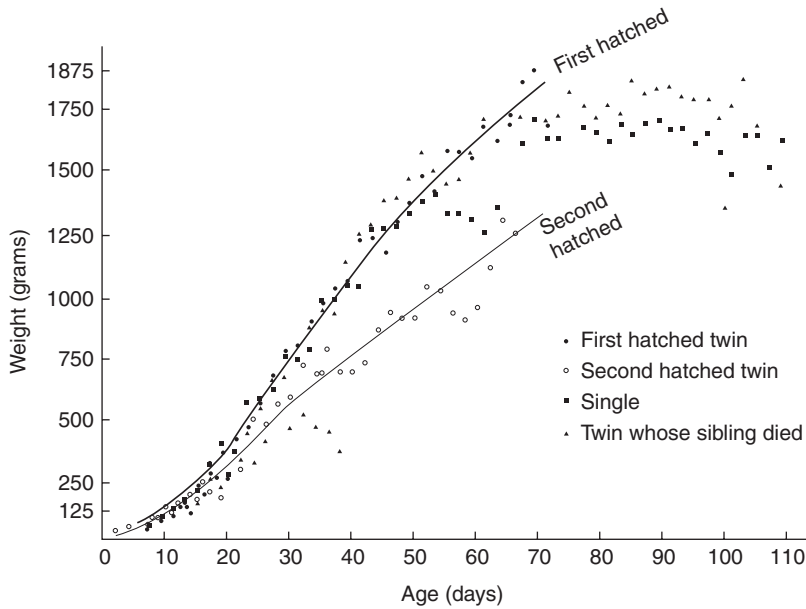
INCUBATION: We gave eggs to a pair that had prepared a scrape but not laid. They reacted by sharing intensive bout of 'showing' and building-in nest-material followed by highly telescoped series of nest-reliefs, performing in a few min that which normally would have taken 2–3 days. Thus got into normal rhythm of behaviour and able to incubate without having laid. Blue-foot often stands off incomplete clutch or leaves it unattended, though this increases vulnerability; also common Isabel. May shade eggs by standing over them or incubate them on top of webs. Nest-relieved bird often departed within secs; usually <10 min. Normally

no physical contact though incomer might display (yes headshake, sky-point, parade, oblique headshake). Occasionally male departed after wing-rattling, returned (landing with foot salute), then departed finally. Incubation period: 41 days (40–3, $n=6$). Incubation shifts: male present 50% of 186 checks, female 53%; av M 18 hours ($n=33$); F 25 ($n=35$).

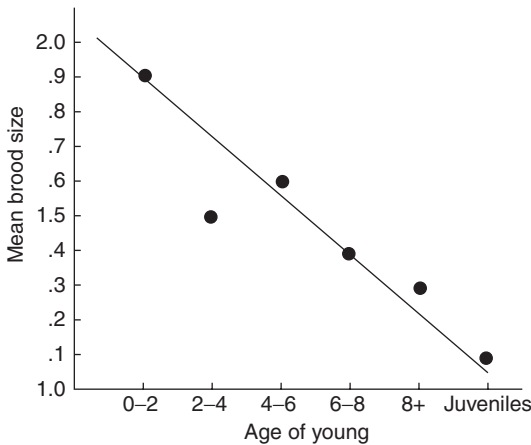
CHICK/BROOD: Hatchling purplish skin with sparse white down on dorsal pterylae and posterior margin of wing. Down thickens; by week 4 chick covered with long white filoplumes. Remains white and fluffy first 6 weeks, then primaries may erupt and first 1–2 mm of tail. At 7 weeks even backward chicks beginning all primaries, coverts emerging, tail may be 60 mm long, forehead clearing. At 10 weeks wing, tail, scapulars well through but down remains thick on head, neck, underparts; thick band follows line of radio-ulna. Forehead may be clear, ear coverts thinning. In some 11–12-week chicks down remains thick on lower back, flanks, undersurface; some on radio-ulna line, top of head, throat, upper breast but forehead, mid-back, scapulars, wings free and ear coverts thin. In others, mere tufts of down on thighs, traces head and neck. At 13 weeks clear of down, almost capable of sustained flight. Gular skin pale blue, bill slightly darker than adult. Legs, feet variable blue-grey (sometimes lilac) turning lighter blue from top downwards. Dark thigh feathers extend to under tail-coverts. Free-flying youngster much deeper brown than adult. Uniformly dark head lacks pale flecks of adult; sharply defined pectoral band.

Growth comparatively rapid. At 65 days some chicks 2,000 g (mean weight adult 1,540 g) but great variability, lightest 60-day chick 47% of heaviest (Hood) but sex differences contribute to this. Also marked regional differences in growth; faster in Peru than Galapagos. Growth strongly allometric; bill conservative in growth even when weight fluctuates. Wing grows from $c.$ 20 mm in hatchling to $c.$ 350 mm at 10 weeks (adult length $c.$ 428 mm).

Torres and Drummond (1999) asked whether the (larger) female received more food than the male but found no evidence. Nevertheless female chicks grew faster.



6.84 Growth by weight of single chicks and two-chick broods, blue-footed booby. From: Nelson (1978b)



6.85 Reduction in brood size as chicks grow older and a proportion of younger siblings starve because of competitive exclusion. (From Nelson 1978b.)

No obligative brood reduction (as occurs in masked booby) but if food becomes limiting 2nd and/or 3rd hatchling(s) excluded by dominant chick and may starve (Drummond *et al.* 1986; Drummond and Chavelas 1989; Anderson and Ricklefs 1992; Guerra and Drummond 1995;

Lougheed and Anderson 1999). Where brood contains male and female chicks, male though smaller remains dominant whether hatching first or second (Drummond *et al.* 1991), *contra* hypothesis that in siblicidal species the smaller individual suffers differential mortality. Lougheed and Anderson (1999) suggest that 'A' chicks attempt siblicide soon after hatching but that parents prevent it. This seems *a priori* unlikely and requires stricter evidence. Torres and Drummond (1997b) examined sex ratio of hatchlings ($n=751$) and found 56% males. At fledging, data over 5 years, sex ratios were similar (1 year) or male-biased (56–70%). Implications unclear.

CARE OF YOUNG: Eggshells removed or tossed away (Drummond and co-workers never saw this). Young brooded continuously for *c.* 2 weeks (change-over took 5–55 sec $n=10$) then guarded until 3–5 weeks; attendance spells av 17 hr males, 23 females. During 1st month (Hood) male present on 44% of 112 checks, female 69%, presumably male foraging more. In 2nd month male attendance dropped to 30% of 161 checks, female 32%. After that adults still spent much time at nest. Even



6.86 Competition for food between siblings here elicits bill-hiding from the smaller, which will probably die (excluded from food) in times of shortage (Galapagos).

when food scarce (shown by growth data) males present 30% checks, females 23%, pair 10%; brooding of chicks younger than 4 weeks dropped considerably, female's more than male's. Chicks 4+ weeks, attended by male on 4% checks; by female 17%. On Isabel one adult present until chicks at least 70 days. As on Hood, females brooded young chicks (5–10 days) more than males and subsequently attended them (up to at least 35 days) as much.

Absences, presumed foraging, 2–12, usually *c.* 4 hr. Single chicks (Hood) fed (*i.e.* bout of feeding) *c.* 2 times per day; much variability (some 8, others none). Some night feeds.

On Isabel, Guerra and Drummond (1995) found that in 1st week parents fed broods at similar frequencies and provided similar masses but subsequently (up to 60 days) females provided more frequent feeds and greater mass than male. These

authors stress that females contribute more to provisioning and that males show no adaptive response, such as more frequent feeds, to young in early stages. They conclude that there is unlikely to be morphologically mediated division in parental care and that, therefore, sexual dimorphism is unlikely to be relevant to this aspect of reproduction. In 1978 I concluded otherwise since feeding niches differ. Seems odd if no related adaptive division of labour.

Male's smallness enables exploitation of feeding niche barred to female whilst her large size maximizes payload. Anderson and Ricklefs (1992) found crop-mass of female >3 times that of male but Guerra and Drummond (1995) (Isabel) showed that sex difference in size did not subtend significant differences in species or, surprisingly, size of captures—Osorio-Beristain and Drummond (1998) on division of labour.



6.87 Smaller sibling dead from starvation (facultative brood reduction; facultative because sometimes both survive) (Galapagos).

Adults will accept strange young up to *c.* 3 weeks but eventually respond selectively to young they have reared and reject strangers.

BEHAVIOUR OF YOUNG: First hatchling does not kill or evict sibling; 2 (or 3) may fledge. But first hatched remains dominant and by competitive exclusion from food may cause death of sibling(s). Drummond *et al.* (1986), Drummond (1987), Drummond and Chavelas (1989), Drummond and Osorno (1992), Nunez-de la Mora *et al.* (1996), Rodriguez-Girones *et al.* (1996) provide details (including physiological) of the mechanism; high cortisone level was a consequence of social subordination. In broods where age differences eliminated by manipulation, hunger leads to establishment of dominance by one chick (Rodriguez-Girones *et al.* 1996). Male chicks, even when outgrown by (later hatched) females, remain dominant. Osorio-Beristain and Drummond (1993) and Drummond and Canales (1998), by cross-fostering dominant and subordinate chicks with singletons (which had not experienced social conditioning) showed that dominants were more aggressive than singletons but subordinates were less so; these differences waned. Anderson and Ricklefs (1995) note that in spite of their capacity to exclude, dominant chicks will allow subordinates to feed even during short-term food shortage. They model that dominants thereby maximize their inclusive fitness. Food-begging

behaviour vigorous and uncoordinated. Lifts wings at elbow joint and moves them spasmodically but not as synchronized flapping. May rotate them forwards as in sky-pointing. Jabs base of parent's bill uttering rapid 'chuck-chuck'. Full-winged juveniles may beg with minor tremblings of outspread wings and head movement indistinguishable from 'yes head-shaking', or with violent flailing and jabbing.

Even downy young may sky-point to overflying adults complete with vocalization and rotation of stumpy wings. By jabbing and 'yes-headshaking' in adult manner chicks from about 6 weeks defend site against adult intruders. But straying chicks may be attacked, even killed.

FLEDGING: Before fledging chick vigorously exercises wings, often becoming airborne. May then congregate at fringe of nesting group. Spends most time near parent's territory and may follow it in flight, attempting to beg on the wing before landing in territory and receiving food. Sustained flight 102 days (95–107, *n* = 8) Hood. Males fledged at 95 days (1,880 g), 98 (1,490), 103 (1,400), 105 (1,550) and 107 (1,570). Females 101 (1930), 101 (1980), 105 (2180). Refers solely to single-chick broods; remarkably consistent considering food short during part of growth. Is sometimes fed at sea, or (Palmer 1962) away from territory; again shag-like.

POST-FLEDGING: Fed at least 4 weeks. One juvenile left Hood *c.* 6 weeks after fledging, 3 others fed 32 or more days after fledging.

BREEDING SUCCESS: Hatched from laid: 72% (*n* = 138, Hood, loss mainly through desertion caused by food shortage, Nelson 1978b). Fledged from hatched: 32% (loss mainly starvation, usually 2nd-hatched in broods of 2, 2nd and 3rd in broods of 3, Hood); 62% (81% male, 74% female (broods of 2); 76% male, 56% female (broods of 3), Isabel, Torres and Drummond 1997a). Fledged from laid: 23% (45% of nests which received egg(s) fledged a chick, low and not representative, Hood). Drummond's figures not given in this form but since fledging success high (62%) and

hatching success likely to exceed 72% of Hood, breeding success probably at least 57%. On Hood out of 71 nests containing 138 eggs, 9 clutches of one produced 1 fledged young, 57 of two produced 29 (although in only 1 did both young fledge), and 5 of three produced 2 fledged young. Productivity highest for clutches of 2. Of the 67 chicks that died, 29 died in their first fortnight. Food shortage played large part in loss of larger young and productivity presumably higher in more normal years or in richer feeding areas (Nelson 1978b: 533–9). Considerable value of 2nd-hatched chick indicated by high proportion of nests holding 2 chicks older than 6 weeks. On Daphne (Galapagos), 2 chicks in 42 of 124 well-grown broods.

FIDELITY TO COLONY, SITE, AND MATE: All first nests of males and females, Isabel, were within natal sub-group (Osorio-Beristain and Drummond 1993). Males and females, respectively, nested at a median distance of 24.1 m (2–110.8) $n=14$ and 28.3 m (4.1–149.8) $n=27$ from birth spot. Subsequent breeding attempts, though at substantial distances from first, still much same distances from natal site. Parents of these first-time breeders themselves subsequently moved on av 26.2 ± 21.2 m $n=21$. Given that median natal dispersal of both males and females carried them past an av 65–90 nests, these authors remark that, as in other birds, close relatives probably do not pair more frequently than estimated

0–3.2%. Figures lacking on fidelity to precise site and mate but Drummond (personal communication) suggests ‘considerable’. Commonly, pairs nest in same spot in consecutive years.

AGE OF FIRST BREEDING: Of 130 chicks marked 1982, 23.1% recorded with eggs or chicks by 1988 after which recruitment to breeding population considered to be at an end (Osorio-Beristain and Drummond 1993). Males first bred at 2–6 years old, females 1–6. Cohorts from different years differed in age of first breeding: females 1982 cohort first bred after 3–6 years (severe ENSO 1982 and 1983) but even birds reared in same season varied by as much as 2 years (males) and 3 years (females). No apparent shortage of sites or mates to account for deferred breeding.

NON-BREEDING YEARS: No breeding during ENSO (Galapagos, Ecuador, Peru).

LONGEVITY AND MORTALITY: Assuming that juveniles return as pre-breeders to natal colony, and that cohort from which they came was representative, the Isabel records (above) indicate that more than 70% die before they can attempt to breed. Seems close to figure for other sulids. More recent work indicates up to 50% of fledglings in a cohort can return to breed (Drummond personal communication). Annual adult mortality of order of 10%.

Peruvian Booby *Sula variegata*

PLATE 3

Dysporus variegata Von Tschudi, 1843, Peruvian Islands

Erroneously *Sula cyanops* and *S. fusca*. Skulls from northern Chile have been named *S. antiqua*.

Other common names: piquero or piquero comun, variegated booby, lancer, camanay (usually refers to blue-foot but in northern Peru camanay = *S. variegata*, piquero = *S. nebulosus*).

French: fou varié. German: guanotolpel. Spanish: piquero Peruano.

Description

ADULT M PRE-BREEDING: Pure white head, neck, underparts. Wings, back burnt brown, variegated due to pale-tipped feathers. Broad white distal margins to fuscous mantle tend to disappear with abrasion giving overall browner. Lower back,

flanks brown sometimes with pale edges to feathers; tail mainly brown sometimes with pale central feathers or pale tips. Bill lead blue, tinged brownish-red—'purplish-blue, sometimes almost pinkish' (Murphy 1936). Facial skin dark grey or bluish, slightly darker than orbital ring. Eye red-brown, sometimes deep orange tint. Legs, feet lead grey or bluish.

ADULT F: As M and similar in size.

POST-NUPTIAL: No obvious change.

JUVENILE AND IMMATURE: Dingy grey to buff or light fuscous below with feathers of breast and belly broadly bordered white after large, sub-terminal brownish area. Somewhat darker band extends from sides of lower neck onto breast, forming pectoral band. Head, neck finely streaked ash. Wings, back duller; darker than adult due to narrower white borders to feathers of dorsal plumage. Iris yellowish-grey becoming light brown in 2nd year, then red. Bill, face bluish. Legs, feet lighter blue-grey than adult's. Acquires adult plumage probably in 2 incomplete moults; intervening stages little different from adult once dull feathers of head and underparts replaced by pure white.

Field characters

Only sulid likely to overlap is blue-footed in which adult's chrysanthemum head and neck feathers diagnostic. In stance and movement Peruvian booby less shag-like than blue-foot but less heavy and deliberate than masked. Carries tail slightly above horizontal but not cocked. Walks and runs easily. Juvenile Peruvian dingy beneath, more uniform above whereas blue-foot dark head, throat, upper breast, and white nape.

Measurements (see Appendix)

Voice

Noisy at colony and when fishing. Males high-pitched bicker and chitter but no piercing whistle. Females grunt and bicker softly, rising and falling in pitch and amplitude, for up to 30–40 separate articulations—usually 6–12. Also loud goose-like honk

(Vogt 1942) or 'cow-call'. Others mention gobbling and trumpet-like calls.

Range and status (Figure 5.14; 6.88)

Off Peru, nests on at least 84 islands, many offshore rocks, and several coastal headlands; mainly 6–10°S and around 13°S, bordering Humboldt or Peruvian coastal current. Main concentrations on Lobos Islands, Mazorca, the Guañapes, Ballestas, and Central Chincha. In 1950 at least 147 islands and 21 mainland localities still yielding guano (Hutchinson 1950); scores more unexploited. Humboldt current supports trillions of anchovies *Engraulis ringens* which formerly sustained enormous colonies of boobies, cormorants, and pelicans (Coker 1919; Murphy 1936; Vogt 1942; and more recently Nelson 1978b; Duffy *et al.* 1984a, Duffy 1994) but gross overfishing has reduced yield and seabirds. Even in 1964–65, there were far more boobies on Guañape Norte and Sur than all the gannets in the Atlantic (Nelson 1978b). Jordan (1963) for 1960 and 1962 (citing only 45 islands and headlands) gives almost 3,000,000 based on 1.5 pairs per m². Peruvian boobies regularly move colonies and new islands can become important strongholds. In 1962 Lobos de Tierra, Lobos de Afuera, Guañape Norte, Guañape Sur, Mazorca, Chincha Norte, and Ballestas each contained more than 100,000 birds. Mazorca held almost 750,000. Then anchovies collapsed in 1972. In 1982 max population Peruvian boobies 6 million, *c.* 50% of total boobies, cormorants, and pelicans. If so, boobies have increased their proportion of population, since these figures (Duffy *et al.* 1984a) differ markedly from those of Jordan and Fuentes (1966). Boobies appear to have become relatively more abundant than other two as overfishing by man has continued; possibly greater foraging range. In 1981 major breeding colonies were on Macabi, Mazorca, Guanape Norte and Sur, Lobos de Tierra, and Santa Rosa (Duffy *et al.* 1984a). In addition (probably small) colonies in Chile and Argentina. Apparent recent increase of sardines *Sardinops sagax* over anchovies though whether (if real) this favours one over another guano species not known.

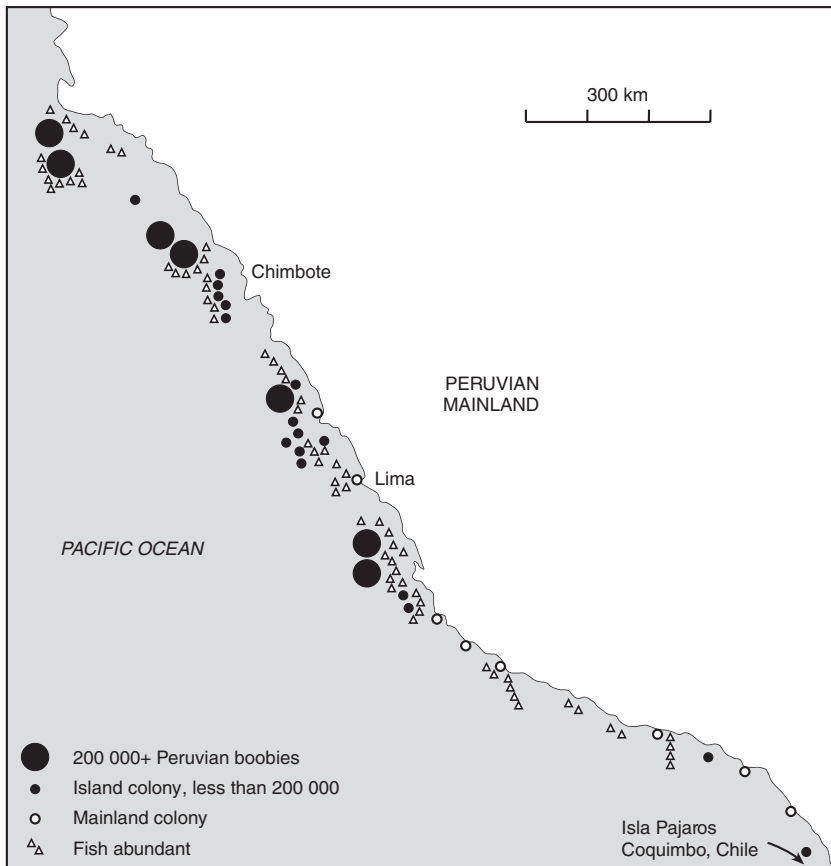
Before man affected guano birds, failure of cold upwelling during ENSO drove cold-loving anchovies too deep for access by seabirds. Resultant

famines, mass mortalities, and abandonment of breeding graphically described, especially by Murphy (1926, 1936). Hutchinson (1950) reviews climatic events accompanying so-called Niño years. The periodic declines in guano birds have not occurred once every 7 years (supposed periodicity of Niño years, speculatively linked to solar events). Nelson (1978b) summarizes material from earlier sources whilst Duffy *et al.* (1994) describe future possibilities for these spectacular islands.

MOVEMENTS: Local and dispersive within breeding range except in famine years, when wanders much further afield and even inland. Between breeding-attempts disperses throughout some 2,250 km of coastal sea, roosting and resting on islands.

Foraging and food

Mainly or entirely diurnal, dawn to dusk, fishing stints usually 2–12 hr. Leaves colony in droves but not in structured processions in which it returns. Unlike other boobies, need not forage widely before encountering shoals but may be seen >80 km offshore. Joins massed ranks of own or other species already fishing. Amazing that those on surface escape impalement. Sometimes fishes solitarily on non-shoaling fish. Dives spectacularly from immediately above surface to *c.* 40 m (av *c.* 15 m). May penetrate deeply or pursue extensively by swimming, remaining submerged for up to 1 min. Hordes may dive simultaneously, but not thought to cooperate in synchronized diving. 'If they chanced to fly over a school of fish, instantly



6.88 Distribution of Peruvian booby on the coast of Peru (1960s–1970s). (From Nelson 1978b.)

and as one individual every booby in the flock (up to 1000) plunged downwards and in a twinkling the air, which had been filled with rapidly-flying birds, was left without a feather' (Chapman 1900). Usual prey so dense and even-sized that sexual dimorphism in booby would be of little value in promoting different feeding niches. Although feeds with other seabirds and among sea-lions and predatory fish, no suggestion of significant dependency.

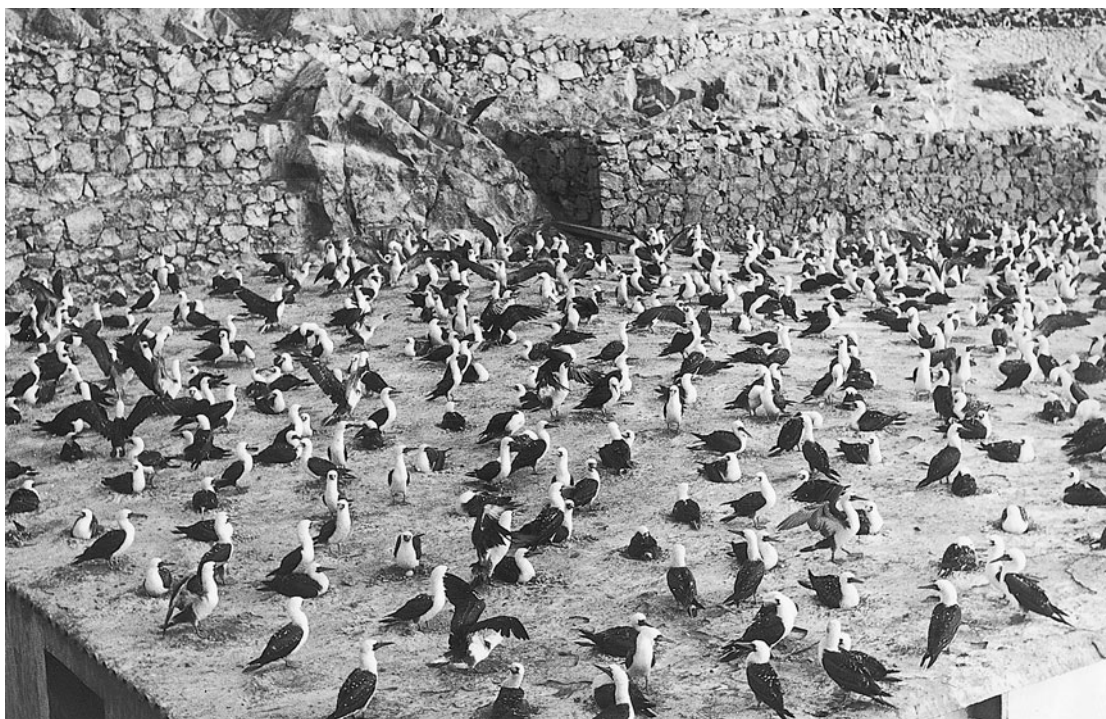
Density-dependent competition for food either with conspecifics or other species normally unlikely but if, after depletion of fish-stocks, competition does occur, greater foraging range of boobies may give advantage over cormorants.

Habitat and breeding biology

(See Fig. at end of 5; Nelson 1978b)

HABITAT: Marine habitat cold, rich upwelling off coastal Peru. Breeding habitat bare, perennially dry,

guano-covered rocks, flat or sloping or cliffs. Can use small ledges or protruberances on sheer faces which demand some cliff-nesting adaptations. When space limited, can utilize whatever offers. On Mazorca many nest on cliffs but spill onto pampa and even onto boulders amidst packed guanay cormorants. In 1907–08 booby almost exclusively a cliff-nester (Coker 1919) but c. 10 years later nesting in great rookeries on flat ground and gentle slopes (Murphy 1936). On specific islands, competition for space between boobies, cormorants, and pelicans leads to fluctuations in their relative proportions. If disturbed, boobies less tolerant than cormorants but more than pelicans. But latter dominant. At one time boobies most numerous of three. Coker (1919) described it as 'almost omnipresent on the Peruvian coast and undoubtedly the most abundant sea-fowl' and in 1920 Murphy agreed. Vogt (1942) ranked it far behind guanay and not far ahead of pelican. Many subsequent surveys showed



6.89 Flat habitat and dense nesting, Guanape Norte, Peru.



6.90 Favoured habitat (slopes and cliffs on Guanape Norte), Note one clutch of four eggs.

that cormorant comprised *c.* 70% of guano birds, booby *c.* 15–20% and pelican sometimes <5%. Currently boobies have increased relative to cormorants whilst pelican population small. Interaction between preferential protection and provision of artificial sites for guanays, as most prolific producer of guano, and natural competition between guano birds, together with unequal ability to cope with decreased fish stocks, must be complex and precludes simple conclusions about relative success of each species.

COLONIES: Largest bigger than any other sulid—up to *c.* 750,000; *c.* 1.5 pairs per m². Minimum width utilizable ledge 25–30 cm usually allows standing off nest.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Peruvian seabirds usually breed annually but short cycle and possibility of laying in any month may enable this booby, under certain circumstances, to breed more than once every year. Claimed (no detail) that after population crash guano birds increase frequency of breeding. Closely related blue-foot can breed at 9-month intervals;

likely that Peruvian can do likewise. But significant proportion of pairs that build do not lay. Whilst neither their status nor state of food resources was known, possible that non-breeding years form part of lifetime breeding strategy. Climate of coastal Peru normally varies little. Oct–Feb air-temperature *c.* 22°C, sea-temperature *c.* 19–20°C. SE Trades blow most of year; normally no rain. But Peruvian booby markedly seasonal, laying mainly Sep–Feb, principally Nov–Dec. Young dependent mainly Jan/ April but some throughout year. Male attends site desultorily until pair has formed, then pair attend for 3 weeks or more before egg-laying. Later, unusual among boobies, attendance continuous; presumably reflects competition for nest-sites.

TERRITORIAL BEHAVIOUR: Site-owning males repeatedly fly out, landing with web-salute (see blue-foot). Female version more muted. Territory defended pugnaciously by overt fighting, sex to sex. Head feathers bristle and birds call loudly, stab, lock bills, and force opponent off site. Fights usually <2 min; rarely damaging. High proportion female–female fights. Ritualized jabbing, sometimes with wing-flailing, repetitive and

rapid (c. 1 to 1.4 per sec). Incorporates withdrawal movement and may be followed by head-shake. Open bills clash and this, with repeated withdrawal, emphasizes stylized nature. Partners jab similarly. At lower intensity involves less jab, more gape, becoming simple threat-gape. Essentially close-range behaviour. Ritualized site-ownership display ('yes' head-shaking) rapid up-and-down nodding.

PAIR-INTERACTIONS: Pair-formation initiated by male 'sky-pointing', simultaneously spreading and swivelling wings. Often, one foot (usually right) spread and lifted. Male whistles, female grunts. After pair-formation, sky-pointing mutual and presumably pair-bonding. Female may sky-point to nearby male; may respond to his sky-pointing by attempting to mount. Importance in pair-context shown by long, continuous bouts, 10 or more per min. Mixed motivation shown by incorporation of jabbing (aggressive), bill-tucking (fear or withdrawal), 'parading' (approach or withdrawal) in mosaic which includes sky-pointing.

Parading is exaggerated walking within territory, lifting spread webs, often 'on-the-spot' with

sky-pointing (Figure 6.91). Bill pointed upwards and/ or sideways or, tucked when parading towards mate. Parading strongly correlated with wing-rattle as precursor of flight. Birds with inhibited flight tendency due to presence of eggs or chicks wing-rattle 6–10 times less often than those on empty nest. In same two groups, wing-flapping used to settle plumage shows no difference. Context of wing-rattling suggests communication: 'I am getting ready to depart' during nest-relief.



6.92 Pair interaction; ritualised mutual jabbing.



6.91 Ritualised pair interaction; on-the-spot parading, adapted from perambulatory parading (cf blue-footed booby) which lack of space here prevents.



6.93 Copulation. Note male does not grip female's head (cf gannet).

Departing bird holds head in extreme backwards position as it runs through neighbours.

In mutual jabbing between mates (Figure 6.92), partners often jab past each other and may reduce jab so much that heads remain motionless but bills open and vocalization remains. Interspersed with territorial display (aggressive motivation) and touching nest-material (conflict behaviour); often terminates with mutual preening, itself sublimated aggression (see Nelson 1978b).

COPULATION: (GFA), Figure 6.93

NEST: Structurally significant mound of guano and detritus *c.* 15 cm high with central cup; excreta used in absence of vegetation but also adaptation to cliff-nesting by cementing nest to ledge. Cliff-nests sometimes break away, despite dry conditions. Fragments of guano, substrate, and feathers used for symbolic nest-building.

EGG/CLUTCH: 60×42 ($53-62 \times 40-44$) $n = 8$; 61.4×42.2 . Estimated weight 50 g. Clutch 1-4, usually 2 or 3. Of 97 nests, 18% one egg, 41% 2, 41% 3. Av completed clutch-size 2.5 (Vogt 1942). My sample: 36% 2 eggs, 53% 3, 2% 4. Clutch 9-10% female weight. Eggs laid 4 or more days apart, incubation begins with first egg. Incomplete clutches never normally unattended.

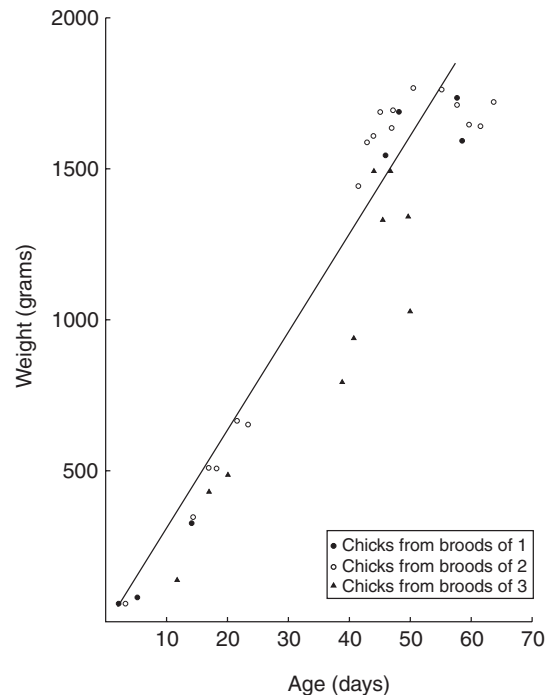
REPLACEMENT LAYING: Lost clutches may be replaced but time intervals lacking.

INCUBATION: Shared, males slightly more. Despite large clutch (often 3, occasionally 4) incubation underfoot still effective though 4 eggs must be upper limit. Change-over 10 sec-2 hr. Incomer may force occupier off nest. Often followed by intensive self-preening, mutual preening, and oiling. Incubation period 40 days (5), 42 (1), 43 (2), 44 (1), 47 (1), 48 (1)—mean 42.4 (8 refer to egg 2, Galarza 1968).

CHICK/BROOD: Hatchling purplish skin; sparsely distributed neossophtiles on back, posterior margin



6.94 In the Peruvian booby unequally sized siblings normally survive because food is plentiful, except in El Niño years.



6.95 Chicks from broods of different sizes showing that brood size has little effect on individual chick growth. (From Nelson 1978b.)

of wing and alula. Eyes closed day 1. Week 2–3 chick well covered in down. Primaries, tail feathers emerge probably week 6. Week 10 wing, tail feathers, scapulars, well-grown but much down remains. Clear of down by week 13. Growth curve in Figure 6.89. Reaches av adult weight week *c.* 7–8 and increases to 120%+ adult weight by *c.* 50–60 days. Then weight falls—feather-growth, wing-exercising—until by *c.* 80 days, well before fledging, chick weighs less than adult.

No significant difference between weight of chick 1, 2 or probably 3 at a given age. Thus, doubtless due to readily available food in most years, later-hatched chicks do not fall progressively behind earlier ones despite considerable difference in relative size. But chick-growth in broods of 3 sometimes poorer than broods of 2. Even if food abundant, limit to how rapidly adults can catch it. But in good year slight difference should not cause broods of 3 to survive much worse than those of 2. Mean clutch-size of 2.5 supports this. In ENSO years all may fail.

CARE OF YOUNG: Brooded until capable of regulating own temperature (2–3 weeks). Brood fed 2–4 times per day. Larger young often unattended during day.

BEHAVIOUR OF YOUNG: Brood of 2–4 chicks live amicably (Figure 6.94). Usually superabundant food seemingly obviates adaptive value of marked sibling-dominance or siblicide. But during ENSO all chicks and most adults may die. Food-begging chick rubs bill up and down underside of long axis of adult's bill. Begging fairly restrained.

FLEDGING: Exercise wings vigorously and essay trial flights by allowing wind to lift them before dropping back on nest (Vogt 1942). Murphy's (1936) account (fledglings tumbling from sky in droves and landing awkwardly far from their nest) anomalous and probably refers to disturbed birds. Vogt describes young attacked and even killed by neighbours if they stray. Fledglings fed only on or near nest. Begins to fly *c.* 14 weeks (Galarza

1968); shorter than other boobies despite large brood.

POST-FLEDGING: Juveniles return to nest to be fed; 4–6 weeks likely.

BREEDING SUCCESS: Hatched from laid: 70–5% or higher. Precise figures unavailable, partly because of disturbance and incomplete observations. Losses due to predation (gulls, turkey buzzards, condors) and displacement during normal social interactions. Fledged from hatched (high to very high in normal years): 78–94% (Galarza 1968). Higher than any other booby and same order as Atlantic gannet which, similarly, is densely colonial breeder in food-rich habitat. Vogt (1942) records that on flat ground on North Chincha, of 1,005 chicks ringed when *c.* 3 weeks, only 6 (less than 1%) died in colony; mortality on cliffs higher due to chicks falling. He inferred this booby not well-adapted to cliff-nesting; understandable if they recently split from flat-ground-nesting ancestor. Fledged from laid: 63% (163 young from 105 nests, productivity of 1.5 young per pair but human disturbance may have lowered it, Galarza).

FIDELITY TO COLONY, SITE, AND MATE: Nesting localities often change between successive breeding attempts though not clear whether would do so if undisturbed by guano operations.

AGE OF FIRST BREEDING: May attend colony in 2nd year and likely to breed at least as early as year 3, perhaps when little over 2 years old.

NON-BREEDING YEARS: No details; some pairs hold nests without apparently breeding.

LONGEVITY AND MORTALITY: No details for annual adult mortality but likely *c.* 10%. In Niño years more than 90% of adults may die. No reliable estimate of pre-breeding mortality; figures suggested (Nelson 1978b) depend on incomplete information; indicate *c.* 50% may die between fledging and breeding.



6.96 Chick begging Peruvian booby. Note guano nest and close spacing.

Brown Booby *Sula leucogaster*

PLATE 5

Pelecanus leucogaster Boddaert, 1783, no locality but Cayenne indicated.

Other common names: brown gannet, black gannet, common booby, Colombian booby, white-bellied booby or gannet, Atlantic booby, Gorgona booby, Brewster's booby. Some names confuse brown booby and brown morph of red-footed booby. Brisson (1760), Andrews (1900), used *Sula sula* for brown booby; particularly confusing since red-foot (*S. sula*) often nests on same island.

French: fou brun, le fou de Cayenne, le fou commun, le petit fou. German: Weissbauchtolpel. Spanish: piquero lardo, bubi chaleco, boba prieta. Other names: pajaró bobo, Alcatraz murgulhao (Brazil), fou capucin (Seychelles), burong bebek (Malaya), tol (Marshall Islands), kiburi (Gilbert Islands), kariga (Tuamotus), keni (Manihiki).

Sub-species

Sula leucogaster leucogaster Caribbean, Gulf of Mexico, tropical Atlantic. *S. l. plotus* vast range from Central Pacific westward into Indian Ocean

and possibly to E coast of Africa, including Red Sea. *S. l. breusteri* arid areas in extreme E Pacific including Gulf of California and possibly E Pacific Islands. Range abuts *S. l. etesiaca* (Colombian booby) of humid zones of Central America and W South America. Last two sharply divided from nominate race of Caribbean by Isthmus of Panama. *S. l. nesiotis* (doubtfully distinct from *S. l. breusteri*) occurs Las Tres Marias and Clipperton. Climatically, Tres Marias birds expected to be *breusteri*; as also on Clipperton (Murphy 1936). *S. l. rogersi*, Western Australia, doubtfully distinct from *S. l. plotus*.

Description

NOMINATE RACE ADULT M PRE-BREEDING: Small; darkish brown upperparts (wings, back, tail), clove-brown head, neck, upper breast; sharp demarcation from white lower breast, belly, under-tail coverts. Clean-cut broad white bar of underwing continues white of underparts to carpal joint. Lesser underwing coverts fuscous. Primaries blackish on outer webs. Secondaries brown, whitish at base and on inner webs. Shafts of new flight feathers blackish, paler when old. Tail feathers brownish black. Bill yellow shading to bluish-horn or pale flesh at tip. Face, gular skin pale chrome-yellow early in season. Eyelids, orbital ring bright blue. Bluish patch in front of eye. Iris variable—dark in Atlantic, pale grey or whitish in South America. Feet chrome yellow.

S. l. plotus (I O): Head, neck darker than upperparts; bill greenish or greenish-blue nearly white at tip; face, gular skin dull purple; eyelids blue; iris grey, yellowish or putty; feet arsenical green or blue-green. Coral Sea: creamy or grey bill maybe tinged yellow or green, rich blue at base; rich blue facial skin, orbital ring; yellow or brown iris; greenish-yellow feet.

S. l. breusteri: Hoary grey head, throat; white chin, forehead, forecrown, ear-coverts shading into pale brownish grey on neck and upper breast. Upper back tends to be pale.

S. l. etesiaca: Grey-headed with almost white forehead becoming grey, then brownish-grey on sides of head and hind neck passing into sooty brown at nape, cheeks, throat. Upperparts, upper breast dark brown, darkest under primaries. Thayer and Bangs

(1905) described *etesiacae* as intermediate between *breusteri* and *leucogaster*.

ADULT F: Larger than male. Plumage similar, soft parts differ less with season; facial skin mainly pale yellow, deeper in courtship. Conspicuous inky patch in front of eye. Eyelids blue. Feet pale yellow, vary little with season.

S. l. plotus (IO): Bill greenish-yellow or greenish-grey, almost white at tip; face greenish-yellow; eyelids blue; iris grey, yellowish-grey, brown or even reddish; feet pale green or yellowish-green. Coral Sea: Facial skin, orbital ring chrome yellow; eye yellow or deep brown; feet chrome yellow.

S. l. breusteri: Head, neck fuscous, distinctly lighter than back.

S. l. etesiaca: Head same as upperparts. Bill sulphur yellow, facial skin pea green or yellow, iris grey, feet yellow.

POST-NUPTIAL: Bill greenish-grey with light tip, fades during incubation; during chick-care, merely whitish with faint blue tinge. Non-breeding facial skin yellowish-green; eyelids, orbital ring yellow. Feet green in parental phase, paler when not breeding.

JUVENILE AND IMMATURE (NOMINATE FORM WITH SUB-SPECIFIC DIFFERENCES): head, neck fuscous, slightly darker than back, scapulars. Fuscous upper breast somewhat demarcated from lower breast, belly, under-tail coverts which are greyish-brown (feathers grey, broad, sub-terminal ashy-brown bar, whitish tip). Tail fuscous, paler at tip, primaries blackish-brown, secondaries like back. In juvenile *plotus* areas brown in adult are dark greyish-brown. Underparts (white in adult) dirty grey; demarcation from breast irregular. All races, underwing bar dull replica of adult's. Neck distinctly darker than back in *S. l. leucogaster* thus differentiating from *etesiacae*. This plumage lasts almost a year; underparts may become darker by abrasion. Spangling on belly becomes bars or crescents by weeks 39–41; 50 weeks after fledging lower underparts more pale than brown. Traces of brown on lower breast and belly until just into 3rd year when may, rarely, breed. Bill dark until 35 weeks after fledging, then turns purplish-flesh, then greyish until well into

year 2 when dull greenish-yellow. In *plotus* grey-blue becomes greenish-grey. Facial skin flesh-coloured in *leucogaster* from post-fledging week 5, then yellow from week 11. In *plotus* at dark grey-blue, then purplish in male, greenish in female. Eyes pale, sometimes flecked. Feet variously pale yellow, light orange-pink or whitish.

Field characters

Sharp demarcation between brown upper breast and white underparts diagnostic in adult. No other adult booby has plain dark brown head and white underparts. Juvenile extremely drab version of adult. Juvenile masked booby, often sympatric, distinguishable by white underparts extending onto throat in inverted 'V'. Juvenile blue-foot shows conspicuous white patch on nape. Demarcation between darker breast and white abdomen much further aft than in juvenile brown. Juvenile Peruvian has more or less uniformly buffish-brown head and underparts. Later immature stages tricky because immature masked booby can develop fairly straight demarcation between dark throat and white upper breast but always much further forward than in similarly immature brown.

Measurements (see Appendix)

Voice

Female—harsh quack, honk or 'a-aark' (almost indistinguishable from female blue-foot); male—sibilant, almost hiss which, during aggression, becomes violent 'chuff-chuff'. Sky-pointing male may utter soft 'iruk iruk'. Intimate pair interactions accompanied by soft, abbreviated calls. Young (both sexes) agonized 'karrk' and rattle mandibles. Male gives female-type call until *c.* 2 years old.

Range and status (Figure 5.14)

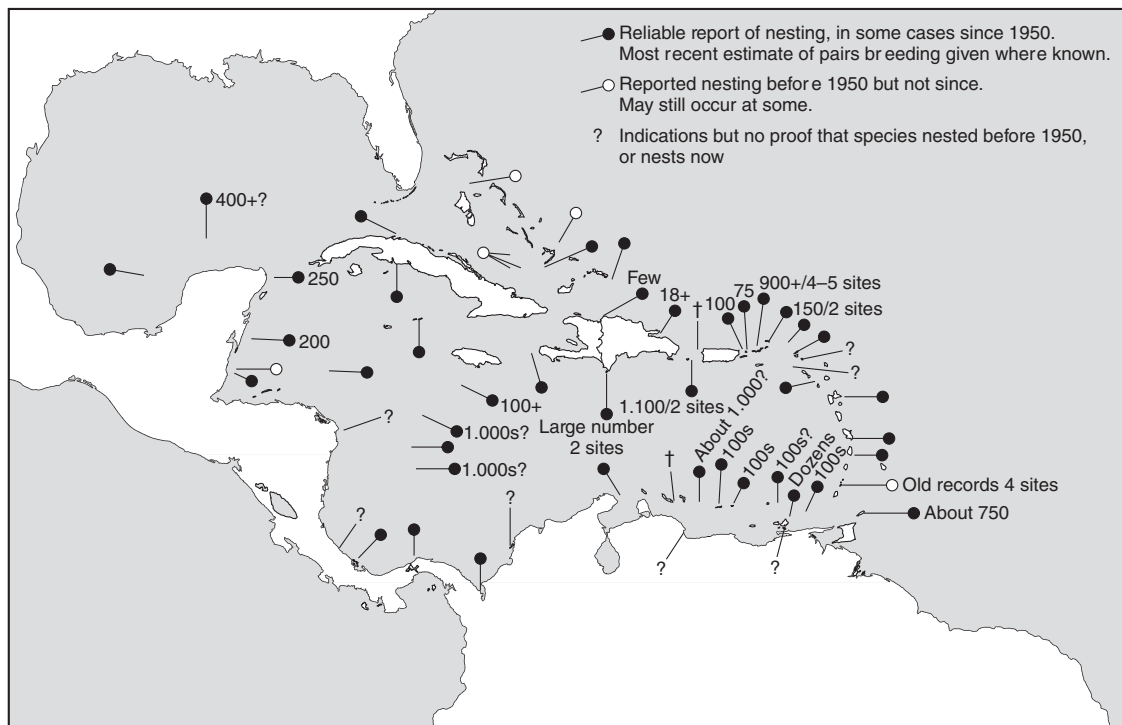
Pan-tropical though thin or absent in Indian Ocean E of Seychelles where might be expected to breed; overlaps with all boobies except Peruvian. Often shares island with masked and/or red-footed. In Gulf California and E Pacific overlaps with blue-footed. Bahamas (most northerly Atlantic station) to Venezuelan islands has been stronghold. W.

Indies to Cape Verdes serves vast area tropical seas; unusually high density of colonies (Figure 6.97). Caribbean population, much diminished. Still nest many islands off NE and E South America. In S Atlantic possibly good numbers St. Paul's Rock. Ascension (Bosun Island and Stack) *c.* 2,000. Thinly distributed Indian Ocean E of Seychelles until Christmas Island (5,000–7,000 pairs). Major colony Pulau Perak now wiped out. Possibly good numbers Manok Island, Banda Sea, but earlier report of huge colony mistaken. Coral Sea, beyond Barrier Reef, nested on 26 of 47 islets and cays (Hindwood *et al.* 1963) but seriously depleted since. In W Pacific much depleted e.g. SW Palau, Helen Island lost 93% seabird population 1979–92 (Keppler 1993). No important colonies central Pacific. Clipperton (E Pacific) major stronghold (15,000+ adults) (Erhardt 1971). None in Galapagos. Major area off Mexico and Gulf of California. Some colonies off W South America, S to equator. Current world population guessed at *c.* 150,000–500,000 adults, but A. Kepler (personal communication)—widely travelled in Pacific—considers this wildly overestimated and substantial decline cause for concern.

MOVEMENTS: Disperses widely (immatures especially) outside breeding season. Occurs in large numbers on many islands where it does not breed. Vagrant well outside normal range, e.g. Mediterranean; recent sightings off North Carolina.

Foraging and food

From close to colony to tens of km offshore. Sex ratio strongly male biased within 20 km of colony, but female (larger) biased beyond 90 km (Gilardi 1992). Solitary or in groups, sometimes large, with other seabirds, feeding on fry driven inshore by predators. Then makes low, slanting dive and may catch a dozen fish in a minute. When hunting so, looks forwards and only slightly down, tacks noticeably and 'winnows' down from 10 m or lower. May dive again almost during take-off, parallel to surface. May fish whilst sitting on water, darting bill beneath surface. Nixon and Lee (1998) recorded almost 50 dives per 10 min on dense shoal but caught fish in only 3% compared with 44% of



6.97 Breeding distribution of the brown booby in the Caribbean (c17,000 pairs). (From Halewyn and Norton 1984.)

less frequent brown pelican dives. Can dive steeply from considerable height. May dive in bow-wave of ships. Can remain submerged for up to 40 sec. Has been filmed banking and turning with great verve underwater using webs and angled wings and steering partly by tail. Lamb (1910) says often fish at night off Mexico. Obtains most of food in open ocean where often catches flying fish in air. Males especially small and light (only male red-foot smaller). Often sits on water juggling catch. Simmons (1967a) emphasizes brown booby's tendency to fish individually, relating this to hunting camouflage and dispersed prey. Flies to and fro in skeins of 2-27 birds. Recorded fishing apparently cooperatively (Lowe 1909); a compact flock manoeuvred as if controlled by one bird. Occasionally feinted, pulling out in unison, eventually diving in concert. Lowe did not record any coordinating vocalization, but Gibson-Hill (1950a) noted calls from fishing birds. Afterwards may raft densely, possibly to thwart attack by frigatebirds. Sometimes try to steal fish from each other or from masked boobies.

Wide spectrum of prey (more than 20 families of fish) but mainly flying fish and ommastrephid squid (Harrison *et al.* 1983; Marchant and Higgins 1990). Mainly small but up to 37 cm and 450 g, but average prey size (Samoa) 6.35 cm. Takes proportionately more small fish than masked booby. If only small fish, av number per sample 20. Few were young of large species, even though samples from terns showed availability. *Almost total overlap in species taken by brown and masked* (Ascension, Dorward 1962) though brown tends to feed on smaller fish. Evidence that brown specialises heavily on different prey at different times.

Habitat and breeding biology

(See Fig. at end of ch. 5; Dorward 1962; Simmons 1967a, 1967b; Nelson 1978b)

HABITAT: Tropical and sub-tropical seas. Marine inshore feeding most closely resembles blue-foot, with which it shares much behaviour. Also like blue-foot often breeds at intervals of less than a year.

In many places true cliff-nesters, using ledges, or preferring rough slopes and cliff-edges. Will use flattish ground and on sandy cays may be in danger of washout. Prefers more vegetated areas than masked booby. Will nest in deep crevices between pinnacles, on man-made structures, totally exposed on rock. Does not nest in true holes or in trees but can perch in them. If sympatric, usually nests discretely but will scatter amongst blue-feet.

Tolerates wide range of climate and environment from wet vegetation on rain-soaked Gorgona to bare, intensely hot rocks in Gulf of California. Plumage differences linked to environment but adaptive significance unclear.

COLONIES: Small or moderate. No extant colony >5000 pairs; previously larger (see Chapter 3, discussion of Colony). Some dense if on flattish ground but most scattered groups with irregular spacing often due to predilection for precipitous terrain. On Christmas Island (IO) groups 2–3 to 100–200 pairs at variable density—inter-nest distance 0.6–27 m. In Bahamas, large colony, nests consistently 2–3 m apart.

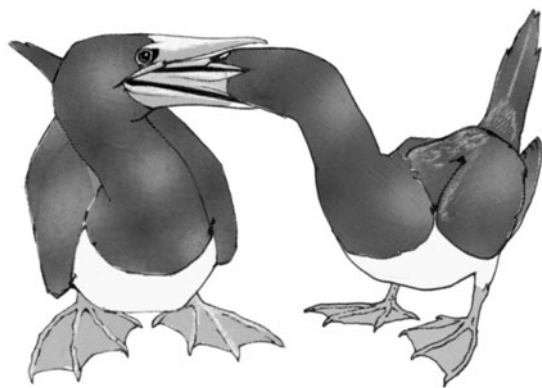
FREQUENCY, TIMING, AND DURATION OF BREEDING: Most extensive evidence of periodicity gathered by Dorward on Ascension (111 pairs over 3 seasons); (see also Simmons 1967b). Established that: can breed successfully every 8 months; some birds miss entire 8-month cycle if forced to miss part, and so remain 'in phase'; birds failing at various stages in cycle can lay again at next peak time because not compelled to take 8 months between successive layings. Birds which follow successful breeding by laying again 8 months after previous clutch forfeit most or all of 'rest period' since full cycle can last fully 8 months. In 26 cases, however, av 5 weeks (0–14) elapsed between end of juvenile begging and next laying. Pairs which fail, even at chick stage, can lay again within a month. In many places broadly, though nowhere narrowly, seasonal. In impoverished, blue-water areas may breed opportunistically when food becomes adequate. Experienced breeders may be seen—e.g. Ascension—in any month (Simmons 1967b) though some colonies may be deserted for period. But

Dorward (1962), also on Ascension, noted that brown boobies mainly absent outside breeding period, gradually increasing overnight presence as next one approached. On Kure Atoll (P O) some present all year (Woodward 1972). Under monsoon regime may desert colony.

On Ascension laying occurred in concentrated bursts as response to food triggers. In locally discrete groups laying often synchronized and out of phase with others in same colony. But in more topographically homogeneous colony may show much greater degree of overall synchrony, which, however, may not be seasonally consistent. For example on Pulau Perak, Malaysia, laying may be concentrated Nov–Jan in one year but Feb–Mar another (Wells 1986). In Caribbean may be 2 clear peaks in one year (van Halewyn 1978).

TERRITORIAL BEHAVIOUR: Agile and displays in flight. Male reconnoitres breeding locality; may attack presumed territorial rival in flight. Male outposts on vantage points; vocalizes and displays to overfliers. Nest-material may be held high whilst bird calls explosively. Intrusion elicits strenuous and prolonged fighting with wing-flailing. Lunging or jabbing interspersed with violent downward movements of partly opened wings and intense calling. During ritualized jabbing head feathers ruffed. Repeatedly leaves site, circles, and flies in, calling; performs post-landing territorial display, swaying head forward, down and from side to side, still calling. Touches nest-material. Forward head-waving may be preceded by intent 'staring'.

PAIR INTERACTIONS: 'Sky-pointing'—male advertising sexual receptivity—homologous with equivalent in other boobies. Typically, only male sky-points. Bill-touching occurs particularly when partners rejoin; whilst still airborne, inflier, vocalizing, points at partner who turns to face it so that bills are momentarily frozen in opposed position. Bills may be inserted. May 'pair-flight' in ritualized manner (slow, exaggerated upstroke). Activities occur in complex mosaic, including ritualized locomotion with associated behaviour such as bill-tucking, bill-raising, and wing-rattling.



6.98 Bill insertion in brown booby. Unusual behaviour for a solid; not courtship feeding. (From Nelson 1978b, drawing: J.P. Busby.)

COPULATION: (GFA)

NEST: Only ground-nesting booby to build structurally functional rather than symbolic nest, from material other than excreta; often essential on cliff-sites. May be considerable assemblage twigs, stems, debris, with semblance of finer materials in cup. Or may lay in mere scrape. Will pilfer. Pair share in ritualized placing of material. Nest-building movements rudimentary, side-to-side quivering, but bonding function evident. May occupy centre in turn, symbolic nest-relief foreshadowing behaviour during incubation and early life of chick.

EGG/CLUTCH: Egg 1 63.4 (58–69) × 42.7 (36–45.3) $n=44$ Christmas Island (I O); 60.0 (59.5–60.5) × 41.9 (41.4–42.5) $n=2$ Willis Island. Egg 2: 60.2 (56.2–65) × 41.1 (38–43) $n=18$ Christmas Island; 58.0 (56.4–59.5) × 42.7 (40.6–44.7) $n=2$ Willis Island. Egg 1 or 2: 60.8 (55.5–66.1) × 41.5 (36.8–44.2) Coral Sea; 58 × 40 Hawaii; 61.3 × 42.8 $n=12$ Marianas; 59.4 (52.5–65.5) × 40.2 (34.5–42.5) $n=40$ Pacific; 53–64 × 37–43.5 $n=30$ Cape Verdes. Weight: Egg 1: 57.3 (40–60) $n=27$ Christmas Island; 62.5 (57.5–65) $n=3$ Willis Island. Egg 2: 53.2 (45–67) $n=20$ Christmas Island; 59.1 (52.5–65) $n=3$ Willis Island. Shell comprises $c.$ 12.5% of egg weight, yolk 16% and albumen 71.5% (shell 8g; yolk 9.6g (8–11), albumen 45.5g (33–51). Egg 1, 4.5% female's weight, egg 2, 4.2%

(Christmas Island). No difference in weight eggs 1 and 2 (Great Barrier Reef, Heatwole *et al.* 1990).

Clutch 1 or 2, occasionally 3 (Ascension normally 2, Dorward 1962); Great Barrier Reef 1 egg (20), 2 eggs (19) (Heatwole *et al.* 1990); Christmas Island (excluding replacements) 1 egg (42), 2 eggs (30), 3 eggs (1) (personal observation); Kure, 4 successive years involving 93 clutches: 1 egg (7.5%), 2 eggs (83.9%), 3 eggs (8.6%) (Woodward 1972). Whilst this gives av 2.1, compared with 1.5 av for 139 clutches from various other parts of its range (excluding those cited above) it is based on more complete observations. On Christmas Island 82% of clutches laid in peak period contained 2 eggs, 18% in those laid outside this period. On Kure 5.2 days (3–9) elapsed between eggs 1 and 2; hatching interval 4.6 days (1–9).

REPLACEMENT LAYING: (Defined as within 6 weeks of loss to exclude possibility of a new breeding cycle.) On Kure fewer than 50% of lost clutches replaced (28 lost, 13 replaced). On Christmas Island 8 replacements took 20, 21, 23, 26 (2), 27, 29 and 30–4 days. On Ascension few failed nesters re-laid (Dorward 1962) but Simmons (1967b) said 5–6 weeks elapsed; no correlation between this period and stage at which previous attempt failed. Repeated replacement (up to 4 times) recorded.

INCUBATION: Eggs often on top of webs. May roll in displaced egg.

INCUBATION PERIOD: Christmas Island 42.8 days $n=5$; Ascension 43–7; Kure Egg 1, 42.4 (39–48) $n=62$; Egg 2, 42.2 (40–4) $n=44$. Thus laying interval between eggs 1 and 2 is preserved, leading to hatching asynchrony.

Incubation shifts vary with season and year: 1–6 hr ($n=38$); 7–12 (35); 13–18 (33); 19–24 (24); 25–30 (4), 37 (1)—mean 12 hr (excluding prolonged spells immediately prior to desertion, Ascension, Dorward 1962); 6 min–12 hr 30 min ($n=195$, Ascension, Simmons 1967b). Change-overs: 48 dawn, 39 07.00–11.30 hr, 34 12.00–17.00 hr, 20 dusk, 2 during darkness.

CHICK/BROOD: Hatching slate-grey or pinkish-mauve, sometimes bluish blotches. Eyes may open



6.99 Older sibling evicting younger (obligative siblicide contra facultative of e.g. blue-foot). (Photo: E. Coelho.)

day 1. Bill pinkish upper mandible, black distally with white tip. Egg-tooth yellow. Beginnings of white down on dorsal pterylae, two tracts on radio-ulna and posterior margin. Week 1 sparsely covered fine white down; bill livid blue-grey; forehead, orbital ring green or blue; throat cream or greenish. Skin visible through down, bluish-green; feet pale green—diagnostic combination. Head skin may be purplish. Weeks 2–4, down lengthens and thickens; chick fluffy white; primaries through at 4 weeks though may remain hidden till week 6, presumably depending on food. Week 5 down full length, primaries (max) 20 mm; juvenile contour feathers emerging. Feathers appear first on breast, abdomen, humerals, later on back. Week 7 (Christmas Island) almost adult-size; conspicuous primaries, scapulars, and tail but in some localities these not be visible. Weeks 8–9 longest primary may be 89 mm, tail 97 mm; forehead feathers sprout; secondaries well-grown; scapulars unite in mid-line. Tail now a strong fan. Week 10, down thinning but still thick on head, neck, thighs, flanks, rump. Pectoral band may be apparent. Week 11 may be clear of down on wings, crown, upper breast though down thick on thighs and flanks until week 12 then clears rapidly—wisps usually until end week 13. Bill now light blue, orbital ring grey-blue, iris light grey, feet greenish.

Like other tropical boobies can survive starvation by slowing development. Growth rate (see Figure 5.27) shows great regional variation. Growth allometric; feet reach adult-size first, then wings, tail, and finally bill; can fly and learn to fish

before bill full-size. Chick from egg 2 normally killed or excluded by first-born.

CARE OF YOUNG: Brooded or guarded for 3 weeks or considerably longer, av *c.* 6 weeks, varying with locality (temperature, shade, food). Brood-spells, Ascension av 12.4 hr (chicks 6–10 days); guard spells 6.8 hr (chicks *c.* 25+ days). Distribution of relief suggests females fish further from base. Male:female ratio of feeds delivered to nestlings 70:125, juveniles 59:127 (Ascension, Dorward 1962). Since female feeds likely also to be larger; they seem to bear most of cost.

BEHAVIOUR OF YOUNG: (See brood-reduction Chapter 3 and Figure 6.99). Strays after 4–5 weeks; may move several metres to shade. Early food-begging as in other sulids; later thrashes wings, bobs head, lunges at adult's bill and calls continuously. Thus not cliff-adapted. Apparently does not bill-hide if attacked by an adult, in this differing from masked and blue-footed. When large, defends parent's territory by jabbing, wing-flailing, and calling. From *c.* 4 weeks interacts with parents (sparring, bill-gripping).

FLEDGING: Gradual if topography permits. Exercises wings, moves to vantage points. Fledging period Kure 95 days (85–103) *n* = 32 (Woodward 1972); Christmas Island (I O) 96 days (87–100) *n* = 11. Ascension 94 days (86–103) for first flight *or* completion of down-shedding (Simmons 1967b); Dorward (1962) *c.* 120 days *n* = 5 but affected by food shortage in later stages.

POST-FLEDGING: Fed Christmas Island and Kure 4–8 weeks; Ascension (equivocal; reckoned as period when juveniles regularly at breeding group) 25 weeks (7–59)—av probably too high. Seen to be fed 6–39 weeks post-fledging though sustained begging seen from juvenile 51 weeks.

BREEDING SUCCESS: (Kure, Woodward 1972; Christmas Island IO, Nelson 1978b; Ascension, Dorward 1962) Hatched from laid: 70.4% (*n* = 71), 58.9 (50), 55 (60), 64.9 (37), 56.4 (55), av 61.2% (combining eggs 1 and 2, Kure); 51% (*n* = 84) (but

68% clutches hatched at least one egg, Christmas Island). In impoverished areas most egg failures due to desertion, as on Ascension, first half Sep 1958 when, during food shortage, 51 of 89 pairs deserted; only 38% ($n = 185$ clutches) produced a chick. No comparable desertion reported in other parts of range. On Kure and Christmas Island cause of loss not obvious but egg 2 sometimes lost after egg 1 hatched, adult's brooding activities either ejecting or breaking it. Sea-swell destroys nests in some locations. Predators can be locally significant. Fledged from hatched (varies greatly with region): 79% (65–96% over 5 years, Kure); 81% (Christmas Island). These latter very high for a booby. Causes of mortality on Ascension mainly starvation (Dorward) or ocean-swell and displacement by adult intruders (Simmons 1967b). Apart from starvation, chick loss mainly in early stages (inadequate parental care and predation). Heavy losses from wild pigs on Clipperton. Human predation and disturbance important. Fledged per pair: 10% 1958 ($n = 185$), 20–6% 1959 (Ascension); Simmons's figures similar; 75% (Kure); 58% (Christmas Island). Only two records of a pair rearing 2 young (Kure and Ascension). Higher productivity of 2-egg clutches than 1-egg not fully accountable on insurance hypothesis (p. 00). On Kure, egg 2 produced a fledgling in 19.2% of pairs (1964), 13.1% (1966). Yet 84.3% 2-egg clutches ($n = 51$) produced a fledgling against 28.6% 1-egg ($n = 7$). Comparably, Christmas Island 75% ($n = 20$), 45% ($n = 30$). Possibly parents of 2-egg clutches more experienced.

Replacement clutches provided 5.8% of 52 fledglings (1964–66, Kure), 17% of 35 fledglings (Christmas Island). Fledglings per clutch: 67%.

FIDELITY TO COLONY, SITE, AND MATE: Marked breeding philopatry. Of 2,044 birds ringed Swain Reefs only 1 (non-breeder) recaptured outwith. Recaptures breeding mainly on island where ringed (167 of 820 nesting adults ringed) but 9 nesting on different island—one 117 km away (O'Neill *et al.* 1996). Similar settlement on Rocas Atoll (Brazil) of birds born elsewhere on Brazilian coast (Schulz 1998). Natal philopatry also incomplete. 3 bred on non-natal island (723 ringed, 32 recaptured). Non-breeding birds recaptured on

different islands within complex, up to 110 km apart. Of 930 young ringed within Coral Sea and Great Barrier Reef, 12 recovered extraliminally—mostly in Papua New Guinea and Solomons. Dorward (Ascension) found that all identifiable individuals used exactly same nest-site in successive breeding attempts. Simmons recorded that 90% of birds with sites which he judged to be favourable and 75% of those he thought unsuitable remained faithful to them, 1962–64. Males showed greater fidelity than females. Fidelity to mate less well documented but probably more than 50%. Of pairs continuously occupying their site, 83% stayed together from 1962–64 (Simmons 1967b).

AGE OF FIRST BREEDING: 3rd year or later. Of 7 birds ringed as chicks on Swain Reef, age first recaptured as breeders: 3 years (1); 4 (3); 5 (1); 6 (1) and 8 (1) (O'Neill *et al.* 1996), though first recapture need not mean first breeding. On Kure most absent for first 2 years, returned during 3rd or 4th. One male bred in immature plumage.

NON-BREEDING YEARS: During unfavourable periods experienced adults may attend colony but without breeding.

LONGEVITY AND MORTALITY: From rate at which birds disappeared from breeding population on Kure between 1962 and 1965, and assuming they had not emigrated or become long-term nomads, 22 out of 23 (95.6%) 2-year-olds which returned to Kure survived a further year and of those, 20 (90.9%) survived another year. Av annual mortality for those two years 6.8% (Woodward 1972). Of 66 adults breeding in 1966, 41 recorded alive 3 years later—av annual mortality 14.5%. But some ringed breeders unrecorded one year, then return the next. Simmons suggests 4.5–7.7% annual adult mortality on Ascension (93.3% of 45 males, 86.8% of 53 females survived from 1962–64). Higher survival figures give life expectancy of *c.* 25 years.

In first year many birds die, become nomadic, or emigrate. Over 6 years 4.6–33.3% of juveniles ringed one year seen year following; sheds little light on mortality rate.

Cormorants and Shags

Double-crested Cormorant *Phalacrocorax auritus*

PLATE 6

Carbo auritus Lesson, 1831, North America.

Sometimes placed in *Hypoleucos*.

Other common names: Farallon cormorant, Florida cormorant, white-crested cormorant, white-tufted cormorant, water-turkey or buzzard. French: cormoran à aigrettes. German: ohrenscharbe. Spanish: cormoran orejudo, cormoril, cuervo marino.

Sub-species

P. a. cincinatus: Breeds eastern Aleutian Islands, east to Yakutat Peninsula, and Alaska (western Gulf). Not Canada.

P. a. albociliatus: Vancouver Island (49°29' N) most northerly extension, south to Gulf of California (Baja California) and Revillagigedos. Also widely in interior and along west coast Mexico south at least to southern Sonora.

P. a. floridanus: North Carolina and Florida south to Cuba. Also Bahamas and Isle of Pines where on San Salvador may be a separate and even smaller race *P. a. heuretus* (Watson *et al.* 1991) whose total population probably fewer than 600.

P. a. auritus: Breeds Atlantic coast between Alberta and James Bay and south from Gulf St. Lawrence to Cape Cod and west to Utah. Comprises 60% of population of double-crested cormorants.

Description

ADULT M PRE-BREEDING: Head, neck, lower back, rump, underparts glossed green; upper back,

scapulars, wing-coverts greyish, with black edges to feathers. Wings, tail blackish. Straggly ear-plumes vary from whitish (W) to black (E). Eye bright green, eyelids blue with (*floridanus*) white spots, or orange-yellow. Gape startlingly blue; lores, face, gular skin orange; bill black mottled grey or yellow, upper mandible pale yellow-blue with darker lines and blotches. Legs, feet black. Sub-species differ in size and shape of crest. N and W populations include larger individuals but extensive overlaps (Hatch 1995).

ADULT F: Similar.

POST-NUPTIAL: After eggs laid loses ornamental ear-plumes, facial and gular skin pales from orange to yellow. Blue gape largely lost.

JUVENILE AND IMMATURE: Head usually brown, pale or dark, merging into mottled whitish throat and foreneck. Upperparts dark brownish, scaly. Underparts variably mottled. Wing and tail feathers fading brown or blackish. Eye grey-brown. Face and gular skin yellowish, latter with dark blotches. Gape flesh; bill brown becoming yellowish beneath. Legs and feet black. Brown and pale parts darken with age and become glossy. Head and upperparts usually mixed brown-black. Crest at first very short. Wing-coverts buff, edged brown, or grey, edged black. May acquire definitive plumage in less than 2 years though often takes longer. May briefly have white filoplumes on head before fully adult.

Field characters

Double crest of limited use since only briefly present in spring. Glossy black plumage and yellow/orange throat and eye-patch good field marks. Young birds paler beneath but still with yellow face. Lack of gular feathers often cited as important feature but some juvenile great cormorants lack this (Richards 1989). Adult greys, out of nuptial plumage, potentially confusable but yellow face less obvious and bounded by white margin. Juvenile greys tend to be whiter beneath with (often) marked pectoral band though these features variable. Neotropical smaller with longer tail and white-bounded gular skin. Flies with kinked neck. Very mobile (flies c80 kph at 2.5 wing-beats per sec).

Measurements (see Appendix)

Wing length, culmen depth and length predict sex 96.5% accuracy (*P. a. auritus*) (Glahn and McCoy 1995). Bedard *et al.* (1995b) found overlap of measurements within broods prevented sexing based on any single character. Live adults readily sexed in hand using wing length and one of central rectrices.

Voice

Alarm grunt and a low croak. In breeding season low, continuous 'ok-ok-ok' in bursts of several sec at 85–90 per min and highly audible. Uttered in sexual advertising position and confined to pre-laying stage. Also low 'tic-tic-tic', hollow clicks, nasal gargle, a 'roar' (cf. great cormorant) 'rr-r-r-ooop' as post-landing or post-hop call. Landing call a sonorous 'a-aark' or 'ok'.

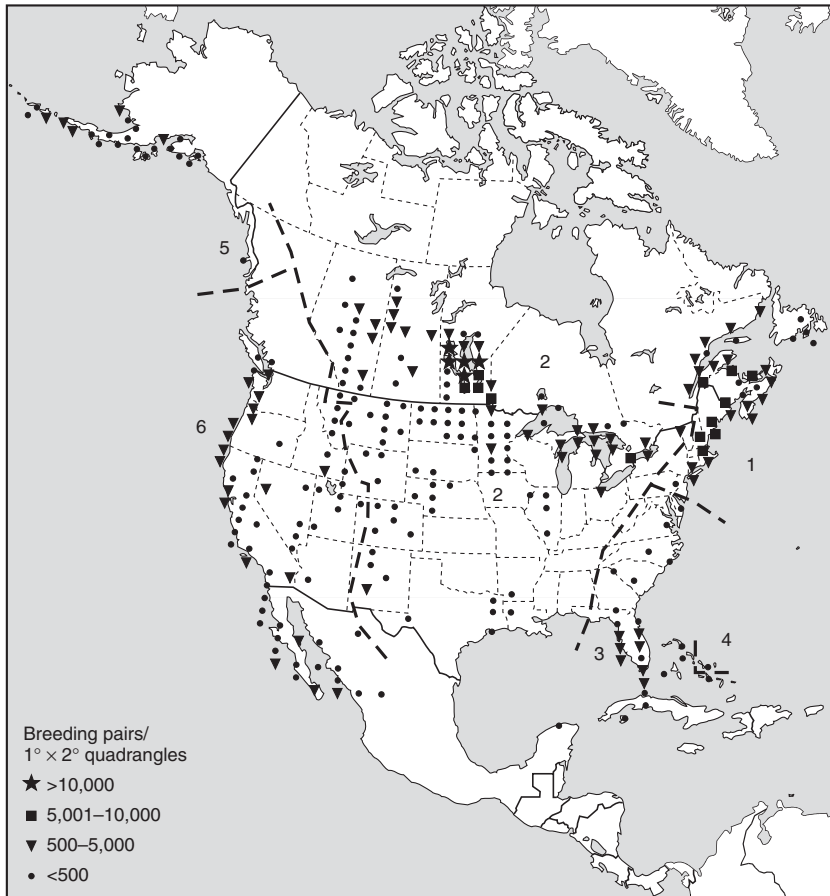
Range and status

(Nettleship and Duffy 1995; *Colonial Waterbirds*, 18, 1995 devoted to biology, conservation, and management of this species; especially Carter *et al.*; Hatch; Nisbet)

Population estimates should be made during nestling stage (Ewins *et al.* 1995).

North American cormorant breeding from Aleutians and Alaska S to Gulf of California and W coast of Mexico (W of Florida outnumbered by

neotropical). Some colonies in E Caribbean. Also from Alberta E to Newfoundland, S to Massachusetts, Long Island, Tennessee, and Texas. Has wider N American range than any other breeding cormorant and only one widespread in interior as well as on coast. Abundant last century but precipitous decline in many areas this century reaching low point 1960s and 1970s, when given 'special concern' status in several states. Decline due to lethal combination of disturbance, heavy persecution, and pollution, especially DDT derivatives, PCBs and dioxin, causing substantial thinning of eggshell and, in places, low or zero breeding success (e.g. Gress *et al.* 1973; Weseloh *et al.* 1983). Then came spectacular increases from 1970s (earlier in some areas) due to protection (some states), reduction in pollution, creation of new irrigation reservoirs and fish-farms, and possibly (in N) amelioration of climate. On Lake Ontario the abundance of alewife (a major food-fish) correlated with increase in cormorants 3 years later (Weseloh and Ewins 1994). Conflict with fishery interests and increasing disturbance combined with improved feeding and some protection has created complex picture with spectacular increases in some areas and overall, but decline or slow growth in others. On upper Mississippi 1980s increase still not returned it to 1940s–1950s levels (Kirsch 1997). Occurs in 40 of 50 States and all 10 Canadian Provinces. Largest populations belong to *P. a. auritus*, including that of N E coast (some 96, 000 pairs) and interior population, centred in N prairies where only cormorant and now outnumbered all other populations combined. Great Lakes alone now hold some 220,000 pairs in more than 100 colonies, with 5,428 nests on Little Gallos (Weseloh and Ewins 1994). Explosive increase (1973–91 more than 300-fold at av annual rate of c35%, meaning doubling of population every 3 years) is thought to have resulted from increased breeding success following decline in pollution, and to increase in food, especially alewife and rainbow smolt (Weseloh *et al.* 1995b). Yet Great Lakes not colonized until some time between 1913 and 1920 (Lake Superior), 1932 (Lake Huron) and 1938 (Lake Ontario). First nesting record for NY State not until 1945. Increases in Lake Ontario showed a consistent pattern of steep increase in one year followed by



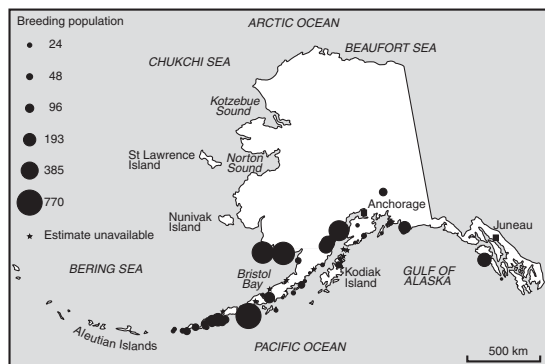
6.100 Distribution of double-crested cormorants in North America. (From Hatch 1995.) 1. Atlantic (NE coast); 2. Interior; 3. Florida and Caribbean; 4. San Salvador; 5. Alaska; 6. West Coast. The symbols indicate number of breeding pairs in quadrangles based on 1: 250,000 maps (1°N by 2°W). The symbols are placed at the centroid of these rectangles.

little change in nest success (Weseloh and Ewins 1994). Order in which lakes colonized suggests eastward expansion of Great Plains population rather than westward spread of Atlantic one (Weseloh and Collier 1995). In and around Florida occurs *P. a. floridanus*, around 14,000 pairs and probably declining. In Bahamas at S E end of its range, population may be *P. a. heuratus* (Watson *et al.* 1991).

On W (Pacific) coast, two populations, Alaskan *P. a. cinnatus* of c. 3,000 pairs at 90 coastal colonies (89% on offshore islands) and *P. a. albociliatus* which stretches along W coast from British Columbia to Mexico (49°29' N to 24°06' N). Further S still may nest in mixed colonies with neotropical cormorants.

Numbers c50,000 birds in estuarine and island colonies, and some in interior. Foxes reduced numbers of Alaskan birds, starting in 1750. Climatic changes may have changed northernmost limits since formerly more abundant at Amchitka Island (51°30' N).

In Oregon abundant in some areas at turn of century but in others didn't nest until 1980 and then, via immigration, increased despite high levels of toxins in eggs. Legal killing ceased 1972 but killing continues nevertheless. Has returned as regular breeder to Iowa. In California expansion began 1960s but by 1974 still small (c600 breeding birds). By 1989 c. 3,250 birds. On Farallons, thousands in



6.101 Double-crested cormorant colonies of Alaska. (From US Fish and Wildlife Service; Alaska Seabird Colony Catalogue.)

mid-1800s but declined to fewer than 100 in 1972. In Mexico early this century Isla San Martin used to hold one of largest colonies in world, at possibly more than 300,000, but disturbance and cats virtually wiped it out by 1977. Some may have emigrated.

Rates of increase of various populations range up to 56% per year (Lake Ontario 1974–82). In Virginia nesting pairs increased from 8 to 402 between 1985 and 1995. In Wyoming population increased from 629 pairs in 9 colonies to 1,477 pairs in 18 colonies in 3 years (Findholt 1988). Throughout North America its median colony size is 101–200 birds.

MOVEMENTS: Resident and migratory. Hatch describes migration patterns for 6 substantially allopatric breeding populations. Seems little inter-mixing between populations E and W of Rocky Mountains. Birds from W of continental divide resident or migrate mainly to W coast; only 5 out of 609 birds ringed in Alberta and none from birds ringed further E recovered W of Rockies (Dolbeer 1991). Migrants from interior populations often follow rivers and by unfortunate coincidence heart of catfish industry is in Mississippi delta at confluence of Arkansas and Mississippi rivers. Cormorants funnelled into area. 20,000–40,000 from Great Lakes and central Canada use upper Mississippi during migration. Highly gregarious; congregate in thousands. In American mid-S birds from widely dispersed areas of

Canada and N USA winter on large, natural lakes and oxbows near Mississippi. Since 1970s wintering cormorants have increased dramatically in delta and nowadays some over-summer, catfish perhaps influencing this. Roosts can contain up to 10,000 birds, which can stay on water overnight. 18 night roosts peaked at 24,660 birds (Apr 1990) and 26,893 (Mar 1991) (Aderman and Hill 1995). Marked birds from Lake Ontario have shown mean recovery distance from birthplace increasing steadily S to more than 1,900 km in Feb–Mar before decreasing to c. 1,000 km (Weseloh and Ewins 1994). Now 40,000–60,000 winter in Texas (Thompson *et al.* 1995). One recorded in Britain (Williams 1996).

Foraging and food

(Nettleship and Duffy 1995)

May forage 30–80 km from roost or colony. Radio-telemetry (18 birds, 400 hr over 36 days) shows mean distance from night roost to first foraging site 15.7 km (3.5–61.8); from forage site to day-roost 2.6 km; between 2 different forage sites 5.6 km but highly variable. Last forage site 11.8 km from night roost (King *et al.* 1995). Av 6.2 foraging sessions per day. Spends c. 1 hour per day foraging at 1.6 dives per min. Mean dive time c. 12 sec but elsewhere may be twice that. Foraging takes 17.7% of daily activity budget (roosting/loading 74.6%; flying 7.7%).

Based on daily energy budget of 1926.7 kJ/g/day and 77% digestive efficiency of fish with av energy content of 4.84 kJ/g, daily fish consumption would be 504 ± 25 g (Glahn and Brugger 1995). Implausibly higher than many previous estimates of c240 g (10% adult weight); 304 g/day (16.9% adult); 208–247 g/day (11.5–13.7%).

Feeds mainly on fish (>29 spp), especially shad (*Dorosoma* spp) and sunfish (*Lepomis* spp). Crustacea (mainly crayfish) locally important; takes amphibia. Some invertebrate prey in pellets comes from fish stomachs (Johnson *et al.* 1997). Food items generally fairly small, especially in females and juveniles (Campo *et al.* 1988); 90% <125 mm and 200 g but will take up to 415 mm. On Lake Ontario consumed less than 1% of small fish, compared with 13.4% taken by sport fish (Weseloh and Collier 1995). Calculated that, feeding preferentially on sunfish

(Beulah, Mississippi), consumed only small percentage available prey and would not affect sport fish (Glahn *et al.* 1998). Most prey little/no commercial value, but growth of aquaculture engenders conflict (see Chapter 4). Blackwell *et al.* (1997) (stomach contents, tidal river, Maine) found salmon smolt common only in May (when among 5 most frequent prey) and highest ranking prey consistently sculpins (Cottidae), sand-shrimps (*Crangon* spp) wrymouth (*Cryptacanthodes*), rock gunnel (*Pholis*), cunner (*Tautoglabrus*). Rail and Chapdelaine (1998) analyse regurgitates in Gulf St. Lawrence; Cairns (1998) reviews cormorant diet NE North America and concludes 44% diet commercial and recreational prey. Where sport fish main prey available, as in trout stocked reservoirs—in e.g. Utah—cormorants have undoubted impact (Ottenbacher *et al.* 1994). Sub-adult rainbow trout, and cut-throat trout 75% (mass) of diet (Modde *et al.* 1996); Lovvorn *et al.* (1999) detected preference for (stocked) cut-throat fingerlings over rainbow. In wild, Birt-Friesen *et al.* (1987) found fish densities significantly lower in bays used by cormorants than in those beyond their foraging range. Concluded that cormorants had depleted their food supply, which would support hypothesis that, during breeding, seabird populations may be limited by food. Much depends on species and circumstance.

Modelling predator/prey stocks on Lake Ontario indicated that 28,000 cormorants during nesting period consume 0.5% of available fish biomass, less than 5% of that taken by predatory fish, some of which may themselves be taken by cormorants (Weseloh *et al.* 1995b). But in 1966, 600 tags from hatchery smolts recovered from 2 Maine cormorant colonies and 11% of 73 shot birds contained tags. Meister and Gramlich (1967) reported 4.9% and 8.1% of 1966 and 1967 fish-stockings in Machias river recovered from cormorant colonies. Although often condemned for taking aquacultured catfish they can be seen to ignore many ponds and settle on a particular one. Have predilection for diseased or dying fish and to that extent may do some good. Big question of whether cormorants lower yield remains open. In relation to salmon, studies suggest heavy predation on wild and hatchery smolts which one would think would lead to fewer adult

fish returning. But opposite correlation has been found, based on number of tags recovered at colonies (minimum predation rate) and subsequent return of salmon. And intensive control of cormorants plus increased numbers of smolt released has not correlated with an increase in number of salmon returning, but with a decrease. Reason seems clear: 'swamping' factors, much more powerful than cormorants or smolt numbers affect return of adult salmon. Yet demand for control of cormorants intensifies. Cormorants do take large numbers of catfish, but eliminate some competition by taking other species such as shad (Hodges 1989). Estimates of losses (c. 4% of catfish standing crop per year) inflated because farmers include losses which would have occurred even without cormorants. Yet 50% catfish farmers in Mississippi delta perceive cormorants as a problem and are dissatisfied with 'fright' strategies (Glahn and Stickley 1995).

Birds collected at fish-farms 1987–88 and 1988–89 contained (biomass) 85.3% catfish, 5.3% gizzard shad, 9.4% bream but variation tremendous—from 0% catfish at some farms to 100% at others. Also varied by month. 74% of samples collected in March, month in which cormorants eat most catfish. In 1989–90 catfish formed 63.9% (biomass), gizzard shad 30.5% and bream 5.6% again with variation from 0–100% catfish. Males caught more catfish (biomass 70.4%) than females (43.7%). Catch rate (av length 12 cm) 5 per cormorant per hour (Stickley *et al.* 1992).

Coastal birds often forage in inshore waters over rocks or gravel but feed also in muddy bays and estuaries where visibility may be down to 30 cm, and in tidal swirls, taking mid-water and bottom-dwelling fish. Dives usually last less than 30 sec but up to 70 sec with surface intervals of 12–18 sec. Feeding depth mainly 2–8 m but may be considerably more.

Forages singly or in flocks, latter, apparently, to some degree cooperative rather than merely communal. Attracted by birds already present, or maybe spotting prey from air, newcomers land and begin to fish. May form long, close line of 50–60 birds, or several hundreds may swim 3 or 4 deep with front birds diving as line advances, then, perhaps, leap-frogging line by flying to regain first

400 Double-crested Cormorant *Phalacrocorax auritus*

6. 102 Diet of the double-crested cormorant. (From Milton *et al.* 1995.)

Prey family and species		Frequency of occurrence (%)	Frequency of numerical abundance (%)
Cod	Gadidae	37.7	43.1
Atlantic cod	<i>Gadus morhua</i>	34.7	39.6
Atlantic tomcod	<i>Microgadus tomcod</i>	1.9	1.3
Pollock	<i>Pollachius virens</i>	0.4	0.7
Hake spp.	<i>Urophycis</i> spp.	2.6	1.2
Sculpins	Cottidae	33.6	17.5
Shorthorn sculpin	<i>Myoxocephalus scorpius</i>	10.8	4.1
Longhorn sculpin	<i>M. octodecemspinous</i>	22.0	12.9
Sea raven	<i>Hemitripterus americanus</i>	0.4	0.1
Herrings	Clupeidae	11.6	6.4
Atlantic herring	<i>Clupea harengus</i>	7.8	4.6
Gaspereau (alewife)	<i>Alosa pseudoharengus</i>	3.4	1.6
Righteye flounders	Pleuronectidae	4.8	2.1
Winter flounder	<i>Pseudopleuronectes americanus</i>	4.1	1.5
American plaice	<i>Hippoglossoides platessoides</i>	0.8	0.2
Gunnels	Pholidae	12.3	16.3
Rock gunnel	<i>Pholis gunnellus</i>	12.3	16.3
Sand Lances	Ammodytidae	5.2	6.2
American sand lance	<i>Ammodytes americanus</i>	5.2	6.2
Wrasses	Labridae	12.3	4.1
Cunner	<i>Tautoglabrus adspersus</i>	12.3	4.1
Smelts	Osmeridae	0.8	0.2
American smelt	<i>Osmerus mordax</i>	0.8	0.2
Freshwater eels	Anguillidae	3.7	2.0
American eel	<i>Anguilla rostrata</i>	3.7	2.0
Sticklebacks	Gasterosteidae	0.4	0.2
Threespine stickleback	<i>Gasterosteus aculeatus</i>	0.4	0.2
Temperate basses	Percichthyidae	0.4	0.2
White perch	<i>Morone americana</i>	0.4	0.2
Butterfishes	Stromateidae	1.1	0.5
Butterfish	<i>Peprilus triacanthus</i>	1.1	0.5
Perch	Percidae	0.8	1.1
Yellow perch	<i>Perca flavescens</i>	0.8	1.1
Catfish	Ictaluridae	0.4	0.1
Brown bullhead	<i>Ictalurus nebulosus</i>	0.4	0.1
Number of samples		268	984

position. Fish silently. Normally 25–30% of all birds are beneath surface at one time and a 6th–7th of all surfacing birds have fish. May mill around then form new line; disperse if prey escapes. Glanville (1992) describes lines of 50–175 birds forming an arc across a bay and driving other birds in front of them ‘in a convulsion of splashing wings . . . to the head of the bay where a frenzy of feeding takes place’. Though largely diurnal, will, rarely, forage at night (King *et al.* 1998). Even within same breeding area, different colonies may differ in foraging areas and diets (Neumann *et al.* 1997).

Apparently not much competition from other cormorant species; differences in ecology and distribution minimize this. Interesting example from Farallons where, relative to other seabirds, has very different diet consisting almost entirely of neritic and estuarine fish captured along mainland coastline and in bays and lagoons. Shiner surf-perch made up 78.6% of diet during breeding season whereas juvenile rockfish, main food of other seabirds, constituted only 1.3% (Ainley *et al.* 1981).

Habitat and breeding biology

(See Fig. at end of ch. 5; review of research needs and recommendations, Erwin 1995; Stenzel *et al.* 1995)

HABITAT: Colonial cormorant breeding from sea level to nearly 2,000 m. Likes islands in freshwater lakes; 52 of 56 colonies in Canadian Prairie Provinces on such islands, 88% of them on ground. Also uses marshes, coastal cliffs, offshore islands, rivers, estuaries. Often nests on rocks, reefs, islets, or steep rocky slopes but also in trees, coniferous or deciduous, dead or alive, although thought that arboreal habitat, in which seems awkward, has been adopted as consequence of disturbance. Recently recorded nesting on powerline towers in Utah.

May nest with other cormorant species such as great, Brandt's or pelagic, and with herons and egrets, anhingas, pelicans, gulls, and terns. When sharing a cliff with pelagics it tends to choose cliff-shoulders and wide ledges, usually high up.

COLONIES: Size presumably related to amount of food within its comparatively short foraging distance.

Range 1–2 pairs (rare)–>5,000. Canadian Prairie Provinces (1967–72) 114 (2–1000 pairs) (Vermeer 1973). Nova Scotia (1971) c68% of 30 colonies held 200 pairs or fewer, range 8–500 (Lock and Ross 1973). Maine (1977) av 149 (1–650, n = 103 colonies) (Korschgren 1979). Alaska (nests): 1–20 (36); 21–40 (8); 41–60 (3); 81–100 (2); 301–400 (1) (Canadian Wildlife Service). Single tree may contain up to 36 nests at various heights. Sub-grouping highly evident; even in crowded ground colonies 4–9 nests usually grouped close together with space between groups. Weseloh and Ewins (1994) found groups of 20 to a few hundred, defining a sub-group as separated by more than 10 m. Unlike great cormorant, groups appear not to change nesting location within general area from year to year but will do so after persecution (Cairns *et al.* 1998). On edges of breeding colonies may be number of pre-breeders or possibly non-breeders, though such birds normally roost elsewhere. Importantly, Palmer (1962) notes that c25% of population at breeding colonies consists of pre-breeders.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually though some doubt as to whether may occasionally produce second brood. Apparently second clutch has been recorded after successful breeding. Range encompasses wide climatic variation and laying season correspondingly protracted. Can be found at some stage of breeding in any month though main laying concentrated in 2–3 month period and, within a particular colony, within 2–3 weeks. On Little Galloo, Lake Ontario, laying began on 19, 20 and 23 April in 1985, 1988 and 1990 respectively though usually marked differences in timing between different years, even in same locality. Laying becomes later as one moves N. Usually marked variation in laying date between and even within colonies due to topography, exposure, age-structure and weather. In Florida laying occurs practically all year though mostly April–June. On Farallons first breeders arrived March and last ones departed Sept. In Alaska birds may not begin to lay until June. As usual in cormorants attendance at colony develops slowly, 1–4 weeks elapsing between first arrivals (males) and nest-building though late-arrivers telescope this.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Male selects territory which may be an old nest or a new site. Overt fighting rare but shows usual aggressive forward stretching and shaking of head with wide gape and hiss and somewhat spread wings. Pair-formation apparently preceded by aquatic display (Palmer 1962) in which male(s) pursue a female on water or in flight. He beats water forcibly, rears up, surges forward in jumps, and plunges beneath surface quite differently from feeding dives. May swim in zig-zag with head and neck submerged, diving frequently and surfacing, perhaps with water weed which he may drop or juggle. Female may dive and handle the weed. Odd that aquatic display seems restricted to so few cormorant species. On territory male attracts overflying or adjacent females using usual cormorant advertising display. Wing-flicks *c.* 1.5–2.0 times per sec uttering synchronized ‘ok-ok-ok’ and pulsating his cloaca. No mention of throwback. In recognition display, ‘gaping’, neck stretched upwards and forwards and male (only) utters a click with each forward movement. Partners may interlock bills and caress heads, bills, and back. In ‘pointing’ oriented towards mate, head and neck waved slowly, sometimes with lunge. ‘Kink-throat’ occurs in both sexes as accompaniment to other behaviour such as nest-worrying and after landing. In latter situation special post-landing posture adopted (forward pointing with neck kinked and bill slightly up). Throughout nesting, nest-touching, neck-snaking, and billing continue to be performed when changing over.

COPULATION: (GFA)

NEST: Can be substantial; sticks (often large), seaweed, vegetation, detritus, with grass-lined cup. 37% of 497 nests in Gulf of Maine contained plastic debris. Becomes fouled and may persist from year to year becoming focus for first-returns though even presence of nests no guarantee that colony will reoccupy that precise location. Substantial nests take >1 year to accumulate and may enhance breeding success. Both sexes build, mainly female. Takes *c.* 4 days. Unmated male

may build and guard against pilferers until he acquires a mate. Material woven in by side-to-side movements of bill; cup shaped by body-movements and tucking.

INCUBATION: Fully shared. Begins with first egg though said to be ‘full’ only after 3rd. Period 28 days *n* = 40; egg 1 29.9, egg 2 28.4, egg 3 27.9.

EGG/CLUTCH: *P. a. auritus* 59.9 × 37.7 *n* = 50; *P. a. floridanus* 58.2 × 36.8 *n* = 46; *P. a. cinnatus* 62.4 × 40.8 *n* = 9; *P. a. albociliatus* 62.9 × 38.8 *n* = 71 (all in Palmer 1962). Weight: *P. a. auritus* 46.1 *n* = 20; *P. a. albociliatus* 51 *n* = 215. Considerable variation in clutch-size; S ones tend to be slightly larger (Johnsgard 1993). Alaska 2.7 *n* = 21, 3.17 *n* = 21; Utah 3.8 (*n* = 76, 2–6, commonest 4); Ontario 3.11 (*n* = 1,022, commonest 3 some years, 4 others); Alberta 3.62 (1988), 2.82 (1990), 2.94 (1992), 3.1 (1993), (1–5, commonest 4). Eggs may be laid daily; usually 2–3 days apart.

REPLACEMENT LAYING: 33–50% of pairs re-nested after loss of nest or eggs (Lake Winnipegosis, Palmer 1962). On Mandarte Island (British Columbia) of 33 nests losing part or entire clutch 29 replaced lost eggs and at another in which 1,691 nests with eggs or young destroyed, subsequent visit revealed that 643 (40%) had rebuilt and laid again (Clapp *et al.* 1982). Av interval between loss of original clutch and replacement 13 days. Repeated replacements may occur (up to 8 claimed but this seems incredible). Drent *et al.* (1964) report max 11 eggs laid by one female. Mitchell (1977) says does not replace clutch unless all eggs lost.

CHICK/BROOD: Hatchling weighs c32 g; 16% still yolk. Naked, with brownish skin darkening to blackish with purple tinge in 24 hours. Eyes said to be closed until day 3. Egg-tooth falls c5th day. Black down appears day 6 first on wing rudiments then behind legs, then on back, rump, lower belly, then other parts. By day 14 covered with short, thick black wool. Day 16–19 pouch yellowish. Primaries erupt day 16–19, 25 mm by day 21–23, 56–62 mm by day

28 by which time entire body becoming feathered though large patches down remain on breast, belly, and back. Sudden closure of nostrils at day 29–30 seems reliable minimum-age indicator. By day 35 down virtually gone from upper surface of wing and from underparts and by day 42 any down restricted to head, neck, and thigh. Day 49 all down disappeared. Day 58 full juvenile plumage acquired. Best criterion for ageing young is length of ulna. Unlike tarsus but like bill it grows most rapidly later in nestling period. Growth extensively charted by Dunn (1975); most rapid in week 2. Weights: 65 g day 2, 80 (3), 119 (4), 158 (5), 435 (10), 841 (15), 1,232 (20), 1,604 (25), 1,801 (35). Clutch takes 2–4 days to hatch so disparity between young, but no marked brood-reduction. Leger and McNeil (1987) report that chicks from eggs 2 and 3 survive as well as older siblings which contrasts with most other studies in other species. Young from smaller broods received same-sized meals as those from larger (see 'Care of young') but for all broods meal-size varied greatly. Before end of nestling period, feeding rate declined slightly whilst weight of each meal did not increase. Consequently estimated total caloric intake per chick declined after about a month. Dunn indicates that young double-crested cormorants gain weight faster, relative to size, than any other species so far studied whose asymptotic weight exceeds 500 g. Asymptotic weight of double-crested is 1,900 g compared with adult weight of 2,047 g. Many other altricial and semi-altricial seabirds, including some pelecaniforms, reach pre-fledging weights well above adult weight, possibly correlated with absence of post-fledging feeding.

CARE OF YOUNG: In no way atypical (see great cormorant and GFA). Brooded continuously for first 12 days except for occasional breaks of 10–20 min. Thereafter daytime brooding declines rapidly and mostly ends at *c.* 2 weeks though nighttime and bad-weather brooding continues for few more days. Young fed *c.* 6 times per day, each time in bouts of usually less than 10 min involving several insertions (see Dunn 1975 for details of feeding frequency and food consumption). Feeding

bouts drop from *c.* 7 to 4.5 times per day between hatching and day 50. Seems that total number of feeds delivered to brood is tailored to brood-size for although single chicks appeared from observation to be fed more often than a chick from brood of 3, difference not significant. Larger siblings of brood fed more often than younger ones but feeding frequency varies widely from day to day. Boluses delivered to chicks ranged up to 100g, meals becoming heavier as chicks grew.

BEHAVIOUR OF YOUNG: Standing, stretching and wing-exercising begins after about 10 days. During week 3 apparent competition among siblings for food becomes marked and begging frenzied. Young void clear of nest and play with nest-material. Late in week 4 begin to wander in increasingly large bands through colony provided terrain allows, meeting little overt aggression from strange adults. But parents rarely feed them except at own nest. By 7–8 weeks fully mobile and fed anywhere in colony, roost anywhere, and highly aquatic.

FLEDGING: Apparently remarkably early at 5–6 weeks (but not flight?) and by 7 weeks can take off from water and accompany adults. Fledging period apparently only 5–6 weeks but perhaps 7 weeks a better figure since by then fully capable of sustained flight.

POST-FLEDGING: Said to be fed 2–3 weeks; unusually short. Young therefore fully independent by *c.* 10 weeks post-hatching, which may be record for pelecaniform with post-fledging care.

BREEDING SUCCESS: Hatched from laid: 54.4–67.5% (Mandarte Island); 54–5% (Utah lake); 35.7% (Ugaiushak Island)—(all suspiciously low, probably influenced by disturbance); 74.5%, 71.8% (Madeline Islands, Quebec Pilon *et al.* 1983). Fledged from hatched: 95% (Mandarte); 72% (Utah). Productivity highly variable partly due to degrees of disturbance and perhaps failure to distinguish between active nests and 'others'. Mandarte Island 2.4 per nest in each of 3 years; Newell Lake,

Alberta 1.9 per nest; Ugaiushak Island 1.43; Lake Ontario (1974–82) 2.8 but 1.9–2.4 during later 1980s. On Farallons 1.29 (1988), 1.13 (1989), 0.61 (1990). San Francisco Bay 0.98 (1988), 1.78 (1989), 1.70 (1990). Presumably linked to disturbance, avian predation is a major cause of failure (Stenzel *et al.* 1995), especially egg-loss due to crows *Corvus caurinus* and small chicks to gulls. Bald eagles also predators, Washington; Arctic fox, Aleutians; coyotes (Saskatchewan); introduced cats, several areas. Other causes of failure include Newcastle disease, infertility or death of embryo, starvation, and displacement of eggs and nestlings due to disturbance (Kuiken *et al.* 1999).

FIDELITY TO COLONY, SITE, AND MATE: Immigration to colonies clearly does occur, probably mainly or entirely of pre-breeders. Whether experienced breeders move extensively is doubtful but fidelity to precise nesting locality far from absolute and therefore neither is fidelity to precise site and to particular mate.

AGE OF FIRST BREEDING: Usually 3 years but sometimes 2. May breed before attaining fully adult

plumage. In slowly increasing Pacific coast population 20%+ only 1–2 years old (Duffy 1995 citing Van de Veen).

NON-BREEDING YEARS: In some areas, e.g. Farallons, most of population may fail to breed in some years, but whether, under normally adequate conditions, a proportion of experienced breeders withhold breeding is not known.

LONGEVITY AND MORTALITY: Potential lifespan 15+ years. Stable populations suggested to show 70% pre-breeding mortality and 15% annual adult mortality. In a Pacific population Van de Veen reported 64.5% mortality during first 2 years of life and adult mortality of 15.1%. Yet Price and Weseloh (1986) try to explain increase in Great Lakes population by suggesting (no hard data) a low (10%) adult mortality and an improbably high (69%) pre-breeding survival. Immigration could be major factor; 36% av annual rate increase at Pigeon (Ontario) over several years (Ewins and Weseloh 1994). Evidence that males twice as susceptible as females to death from culls.

Neotropic Cormorant *Phalacrocorax brasilianus*

PLATE 6

Priority *Procellaria brasiliiana* Gmelin, 1789, eastern Brazil. See Browning (1989) 'The correct name for the Olivaceous cormorant'.

Sometimes assigned to *Hypoleucos*.

Other common names: olivaceous, bigua or Brazilian cormorant, Mexican or Sonora cormorant, black cormorant, and various names derived from pig-like vocalizations such as grunting duck, filthy duck.

French: cormoran vigua. German: olivenscharbe, biguascharbe. Spanish: cormoran bigua, cuervo de mar.

Sub-species

Probably an allospecies of a superspecies containing double-crested cormorant with which it marginally overlaps (Telfair and Morrison 1995).

P. b. brasilianus Panama to Cape Horn. Fuegian population sometimes recognized as *P. b. homensis*.

P. b. mexicanus New Mexico, Central America, southern USA, Bahamas, Cuba. Not separable in field but smaller than *P. b. brasilianus*, with longer bill.

Description

ADULT M PRE-BREEDING: Mainly deep, glossy black including underparts. Long tail (12–14 feathers). Upper back, wing coverts and scapulars greyer or browner with black margins. Nape feathers slightly elongated. Orange-yellow gular skin which has narrow strip of white feathers at margin, ending in a point. Narrow tuft of white feathers and line of small white filoplumes above the ear and a few on neck. Eye blue or green, eye-ring yellow/orange (duller except in peak condition), bill brown or black with

yellowish cutting edge at base of upper mandible, patches of orange-yellow on lower. Legs, feet black.

ADULT F: Similar.

POST-NUPTIAL: Lose white filoplumes during incubation, soft-parts become dull.

JUVENILES AND IMMATURES: Juvenile brown all over body with blacker wings and tail but abrasion soon reveals paler bases of feathers on underparts. Bill brown. Eye brownish and soft parts dull yellow or buff. Post-juvenile plumage similar but gular skin develops white border and underparts become whiter and more blotched. Eye becomes green. Full adult plumage perhaps attained at 2 years. Many details of appearance in various stages of moult, etc. in Telfair and Morrison (1995).

Field characters

Only wholly dark cormorant in South America (despite name, plumage not olive-coloured). Differs from larger and bulkier double-crested,

which, also, is shorter-tailed. Gular pouch of neotropic is backward-pointing 'V', small, pale yellowish and bordered by thin white line. That of double-crested is larger, rounder, brighter orange/yellow and lacks white border. Later immature, but not juvenile, also distinguishable by whitish gular border and brownish-white foreneck and underparts. Patch of skin above lores is brighter yellow in immature double-crested compared with neotropic. Flies with head slightly above neck.

Measurements (see Appendix)

Voice

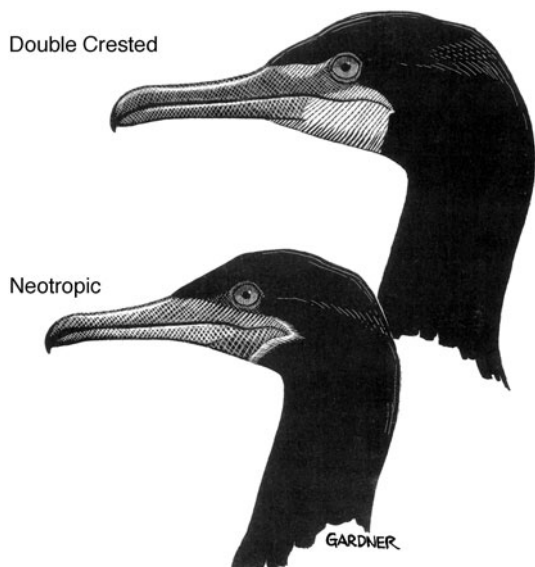
Low, guttural grunts or croaks (alarm), also when fishing communally. So porcine as to deceive those who hear it (Murphy 1936). Usually silent out of breeding season. Male more vocal than female.

Range and status

Widespread in neotropic area; only cormorant ranging from Tierra del Fuego to southern USA, New Mexico, Bahamas and Antilles, hence its now-accepted name. In N America breeds and largely resident along Gulf coast of USA from SW Louisiana through Texas, and from Central Mexico through to Central America. Has recently bred in north-central Texas and New Mexico (Clapp *et al.* 1982; Telfair and Morrison 1995). First breeding record for Arkansas 1998 (Coldren *et al.* 1998). In NW Caribbean breeds on Cuba, Isle of Pines and San Salvador (Bahamas). Breeds throughout lowland S America and up to 5,000 m in temperate Andes. Also on islands off northern S America, thus demonstrating enormous climatic toleration and diversity of habitat. Heading for extinction in Argentina (Benstead *et al.* 1998).

Within USA Clapp *et al.* (1982) give figure of 6,850 breeding birds in Louisiana and 2,550 in Texas (1976 census). After serious decline in 1960s (pesticides and development) both populations steadily increased. In 1990 Louisiana population estimated at 2,755 birds in 10 colonies (Martin and Lester 1990) and in Texas 4,334 pairs (Telfair 1995). Currently breeding population in Texas averages at least 1,200 pairs and in winter about 500 birds.

Most numerous cormorant in S America; population unknown but substantial. Colonies in Bay



6.103 The difference in the profile of the gular pouch of double-crested and neotropic cormorants. (From Telfair and Morrison 1995.)



6.104 Distribution of the neotropic cormorant in North America. Dashed line shows limits of post-breeding dispersal. Breeding colonies are very locally distributed away from coastal areas in the USA. Breeds along interior river systems in central Mexico. (From Telfair and Morrison 1995.)

of Panama contain at least 150,000 adults (Montgomery and Murcia 1982). Further details of population trends in Telfair and Morrison.

MOVEMENTS: Sedentary throughout most of breeding range but in some areas disperses widely after breeding. Northern populations migrate southwards, few birds remaining north of 27°N during winter. High-altitude populations may move lower. Recoveries of birds ringed as chicks in Texas showed only local dispersal up to c70 km but first-winter birds seen up to 500 km S of natal colony.

Foraging and food

Highly versatile in feeding ecology. In marine habitats a bottom feeder in shallow inshore water,

taking prey less than 6–25 cm. Inland, concentrates on small, abundant prey in restricted waters rather than large, dispersed items. Telfair and Morrison (1995) give prey dimensions as 1.8–23.8 cm (c90% approx 8 cm) and weight 0.3–38 g (see these authors for list of prey and other details). Takes whatever most available locally—amphibia, insect larvae, crustacea, chitons and molluscs, though some may have been ingested via fish stomachs. At a lake in Texas 65% of prey items and 37.4% of prey-mass consisted of a single species, the sail-fin molly *Poecilia latipinna* (Morrison *et al.* 1977). Almost all other prey came from 5 groups common in area and characterized by wide tolerance of salinity and water temperature. In Peru seen to catch 22 fish in 10 min,

probably shore-eels *Opichthus* or *Gymnothorax*. When swimming, may be awash before diving from surface. Submergence-time variable, matching depth at which feeding, from average 6 sec in shallow pond to 30–60 sec in sea (much longer submergences anecdotally). Mainly solitary feeder though often in small groups. Bent (1922) described apparent cooperative fishing in Mexican mountain streams, birds forming line across current and beating water with wings before diving. In Texas small flocks formed, apparently when solitary birds chanced upon concentrations of fish at low-tide and resultant commotion attracted others. However, during one 50-hour period of observation flock-feeding accounted for mere 3% of total feeding time. May enter water from air, presumably after spotting shoal. Flies low over surface and dives obliquely into or in front of breakers or into calm water, wings held against body. Such dives superficial, mean duration merely 1.7 sec (Duffy *et al.* 1986). Low success rate. Foraging success of adults 17.7–18.5% compared with immature's 9.9–12.1% (Morrison *et al.* 1978), difference persisting into first winter. Although immatures spent only as much time fishing (total) as adults they fed twice as often. Adults captured prey (success/min) at 0.55 and 1.19 (two different sites) against 0.28 and 0.92 for immatures. Feeding periods per day vary from 3 to 8. May begin soon after sunrise, leaving singly or in groups up to 23. After initial feeding, adults often loafed for up to an hour but after subsequent bouts returned to colony without much loafing. Ceased foraging within hour of sunset and not seen to feed at night. Older chicks and adults regurgitate pellets approx. once per day.

Habitat and breeding biology

(See Fig. at end of ch. 5; especially Morrison *et al.* 1979; Telfair and Morrison 1995)

HABITAT: 'It ignores both altitude and latitude . . . not only does it occur along the sea-coasts but also up the course of almost every river to its headwaters. It breeds on arid islands that lie in front of desert shores, among the trees of steaming tropical swamps and lagoons, on cold beaches . . . soaked by the nearly

perpetual rains of the west-wind zone and on the banks of lofty mountain lakes such as Titicaca and Junin. In short, it exhibits a diversity of habitat and a climatic toleration which are perhaps without parallel' (Murphy 1936). Overall probably favours fresh and brackish water though many occur in inshore marine waters. Well adapted to arboreal nesting, sometimes at height, but also shrubs, rocks, or bare ground.

COLONIES: Size highly variable. For North America Johnsgard (1993) gives (birds not pairs): 1–50 (1), 51–100 (4), 101–200 (1), 201–500 (3), 501–1,000 (3), 1,001–2,000 (1), 2,001–5,000 (1). Some colonies in trees (may be several nests per tree) number thousands and excreta may kill all surrounding vegetation. Will mix with other nesting waterbirds.

FREQUENCY, TIMING, AND DURATION OF BREEDING: No evidence that breeds successfully more than once a year. May lay any month though with well-defined peaks in some areas. In Texas lays early Feb–mid-Oct, mainly May–Aug with, at least in some years, peak first half April. In Patagonia, in Feb, nests contained young of various ages showing that eggs had been laid at least Nov–Jan.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: No details of territorial behaviour. Male's advertising display conforms to basic cormorant pattern (GFA). Wing-flicking occurs in bouts of around half a minute at *c.* 1.7 'flicks' per sec. Each raising of wing tips accompanied by loud vocalization. Upward-pointing head moved out of synchrony with wings. Then a throwback takes head right back to tail. Existing accounts don't say whether head then rotated. 'Gaping' (both sexes), 'pointing' (both sexes), 'kink-throating' (both sexes), the elongated pre-take-off posture with raised crest feathers (and depressed hyoid?) and post-landing posture with neck high and forward stretching, bill-gaping and 'discoidal head' all occur much as in most other cormorants. Murphy particularly notes marked drop in gular region just before landing, even at a roost. No precise contextual details for these displays; likely to conform to familial pattern.

COPULATION: (GFA)

NEST: When in trees, usually in fork, nest is of sticks or twigs lined with e.g. coarse grass. On

coast and artefactual sites may build bulky nest of aquatic plants.

EGG/CLUTCH: $54.54 \pm 2.17 \times 33.68 \pm 0.86$; $54.43 \pm 2.69 \times 33.43 \pm 1.11$ $n = 83$ (Texas pre-1947); $53.55 \pm 1.94 \times 33.94 \pm 0.99$ $n = 7$ (Texas post-1947). Shell weight: 3.01 (2.50–3.48) pre-1947; 2.74 (2.57–2.91) post-1947. Shell thickness pre-DDT (pre-1940): Sydney Island mean 0.328 $n = 75$; post-DDT (post-1970) 0.323 $n = 24$ (1.5% thinner). 1976–77 mean 0.341 $n = 21$ (4% thicker than pre-1940 and 5% thicker than 1970). Thus no apparent effect of DDT (Telfair and Morrison 1995, also concentrations of DDT derivatives given). Weight: egg 1 35.05g; egg 2 34.69; egg 3 32.54 (Sydney Island). Clutch 2–6, usually 3 or 4. Mean 2.99 and 2.87 in same colony, successive years, Texas and 4.02 (2–5) $n = 48$ Louisiana to El Salvador. Eggs laid at 48-hour intervals.

REPLACEMENT LAYING: Common after loss of clutch or part. Interval: mean 8.5 days (2–20) after loss of clutch and 5.5 (1–11) after loss of part; unclear how judged that egg laid 1 day after partial loss was a replacement! Said not to re-lay after losing young. Little difference in clutch-size between original and replacement.

INCUBATION: Period av 24.6 days, beginning with 2nd egg. Eggs hatch asynchronously over several days though presumably some telescoping.

CHICK/BROOD: Hatchling dark grey, soon covered with blackish down. No details of growth and development or brood.

CARE OF YOUNG: Shared. Young chicks brooded continuously; fed several times per day (3–8 bouts?), up to 12 insertions per bout. Said to feed small young by dripping liquid from bill-tip into chick's gape. Feed older chicks much less often. Shade chicks in hot weather.

BEHAVIOUR OF YOUNG: Begin swimming and diving near colony by 8 weeks.

FLEDGING: Begins swimming and diving by 8 weeks. Not clear at what age sustained flight attained.

POST-FLEDGING: Fed until *c.* 11 weeks old and independent by 12 weeks. May then move away from natal area.

BREEDING SUCCESS: Hatched from laid: 57.6% ($n = 55$ nests), clutches of 4 hatched 62.5% ($n = 10$), Sydney Island, Texas, Morrison *et al.* 1979; 98% (Henderson County, Telfair 1995). Fledged from hatched: 57% (Sydney Island); 92.3% (Henderson County). Fledged from laid: 33%, 1.65 per nest (Sydney Island); 2.4 per nest (Chambers County, Oberholser 1974). Mean brood-size (presumably at fledging) 2.94 ± 0.93 (1–5) $n = 254$ broods (Henderson County, 1981–84).

Eggs lost due to displacement and failure at hatching. Many (up to 20%) may just disappear, cause unknown. Most predation follows disturbance and predators include raccoons and grackles. Morrison *et al.* (1979) give 46% of nestling loss as due to starvation and trampling, 33% disappeared and 21% fell.

FIDELITY TO COLONY, SITE, AND MATE: Of 66 colonies in Texas only 7 consistently re-established each year for more than a few years and no detectable pattern showing influence of location or year. Typical phenomenon in cormorants. May re-use same site or may change. Monogamous usually only for one breeding cycle. No information on natal philopatry but clearly likely to be very weak.

AGE OF FIRST BREEDING: 1 year $n = 15$, 2 years $n = 11$, 3 years $n = 5$. All records refer to colour-marked birds attending nests with eggs or young (Telfair 1995).

NON-BREEDING YEARS: Not known to occur.

LONGEVITY AND MORTALITY: No quantitative information but one bird 12 years 7 months. From ringing recoveries, age at time of death: <1 year $n = 5$, *c.* 2 years $n = 1$, 3–4 years $n = 1$, 3.8 years $n = 1$, *c.* 6 years $n = 1$. Only 0.9% of birds ringed, recovered.

Little Black Cormorant *Phalacrocorax sulcirostris*

PLATE 6

Carbo sulcirostris Brandt, 1837, New South Wales, Australia.

Other common names: little black shag.

French: cormoran noir. German: schwarzscharbe.

Spanish: cormoran totinegro.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Overall black, sometimes with purple or green gloss; feathers of upper wing coverts, upper back and scapulars grey with broad black borders giving patterned appearance. Head feathers with narrow pale edges and sometimes a few white filoplumes behind ear and scattered on head and hind-neck. Facial skin bluish or purplish and gular skin violet, appearing very dark. Eye deep green with blue-green orbital ring. Bill dark, slate grey with dark ridge; base of lower mandible blue. Legs, feet blackish.

ADULT F: Similar.

POST-NUPTIAL: During incubation loses nuptial plumes, plumage abrades to duller black-brown.

JUVENILE AND IMMATURE: Dark brown fading during first year as adult plumage begins to appear without noticeable intermediate stages. Iris brown.

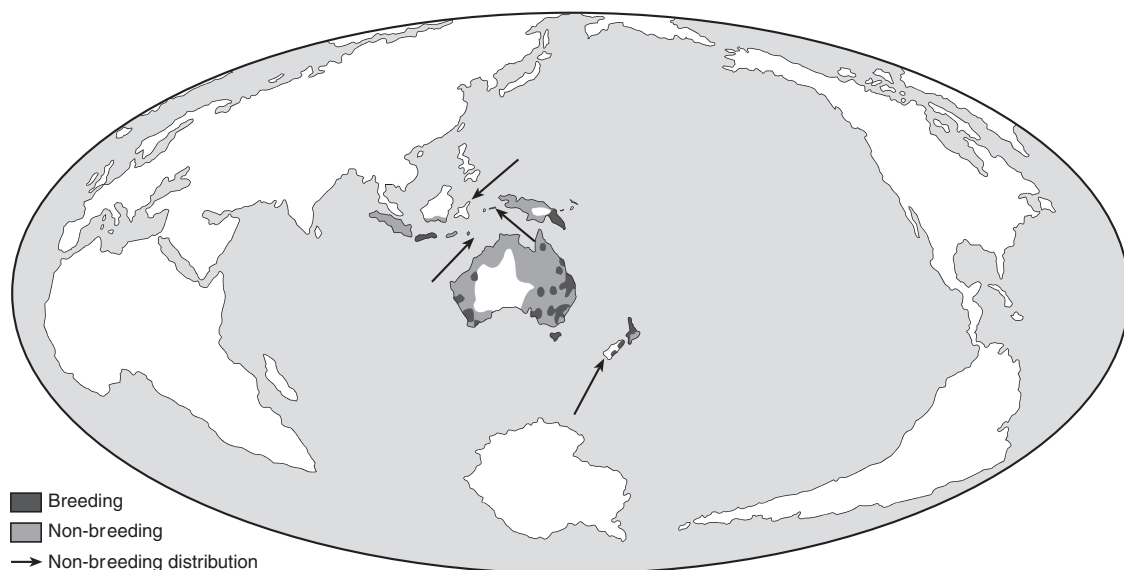
Field characters

Small, slender cormorant with noticeably thin bill. All dark, with dark purple-grey facial skin and dark bill. In Australasia overlaps with great cormorant, little pied, and, very locally, with Stewart Island shag but all these have distinctive characters. Juvenile little pied totally dark but thick bill and longer, wedge-shaped tail aid identification. Javanese cormorant, too, all dark but has yellow bill.

Measurements (see Appendix)

Voice

At breeding-site males bark hoarsely 'hack' during display 'throwback' followed by di-syllabic 'ak-he'



6.105 Distribution of the little black cormorant. (From Marchant and Higgins 1990.)

during head rotation. Croaks harshly during threat. Repetitive ticking 't-t-t' during pre-movement and loud bark 'krah' after hop. A whistling 'tu-tu' during some pair interactions. Female largely silent.

Range and status

Australia (in some areas widespread and common), Tasmania (increasing since mid-1970s, Johnsgard 1993), New Zealand (not common, *c.* 1,000–5,000, more so in North than South Island where not often seen but may be increasing), Indonesia, New Guinea, and islands of SW Pacific. Size of populations not known but certainly many thousands in Australia. Mean densities of 1–2.4 birds per km² reported for riverine area of Northern Territory (Marchant and Higgins 1990).

MOVEMENTS: At least some birds disperse widely during winter. For example Rotorua birds (N New Zealand) go as far as Hauraki Gulf and Wellington. Some dead birds turn up on beaches as far S as Canterbury, though usually rare S of Marlborough–Nelson. Dispersive in Australia, large numbers moving especially when drought follows wet period (inland). Dispersal to coast may then extend to overseas (Marchant and Higgins 1990).

Foraging and food

Exclusively diurnal cormorant reputedly not only communal but also cooperative feeder, 'herding' or encircling schools of fish for which large feeding rafts most efficient. Where food abundant, such flocks may number several hundred birds (up to 1,150 recorded). Move slowly over surface in leap-frogging movement. Eat mainly fish, particularly smelt, carp (sometimes 100%) and perch but, hunting singly, take also freshwater crustaceans (3.9–24.8%). Together with little pied and great cormorants caused almost total depredation of fry and fingerlings of silver perch (*Bidyanus bidyanus*) in heavily stocked ponds (up to 60,000 fish per ha) (Rowland 1995). Details of diet in Marchant and Higgins (1990). Dives not particularly deep; in water 1–2 m av duration 1–4 sec increasing to 19.3 sec in deeper water. Fish usually impaled behind gills, brought to surface, and turned for swallowing. Bathe vigorously after feeding, thus initiating mass preening and wing-drying.

Habitat and breeding biology

(See Fig. at end of ch. 5; Marchant and Higgins 1990)

HABITAT: Versatile cormorant of sheltered coastal waters, especially estuaries and coastal lagoons, and of wetlands. Inland, tends to prefer waters more than *c.* 1 m deep in fairly large open stretches such as lakes, rivers, swamps, including mangroves, with open water. Common on artificial dams etc. Nonetheless does occur on shallow and transient waters and in densely vegetated swamps and channels. Occasionally forages around offshore islands. Thus widespread and occurred in higher proportion of survey blocks in Australia than did any other cormorant except little pied (Blakers *et al.* 1984). Aerial surveys in E Australia showed 45% of population on artefactual waters such as dams and 90% occurred on wetlands of less than 100 ha (Marchant and Higgins 1990). Breeds mainly in swamps and on freshwater lakes preferring trees surrounded by water in remote wetlands. Apparently does not nest on ground. Adjacent feeding important and breeding inhibited if surrounding wetland unproductive, as when recovering from drying out.

COLONIES: Typically contain fewer than 100 nests, presumably variably spaced (no information on actual densities). Marchant and Higgins cite evidence of 'thousands' of birds at colonies but this, presumably, does not mean similar number of nests. Interesting reference to 'discrete flocks of up to 30 birds' arriving at colony and forming 'sub-units' nesting close together and in synchrony. Poses questions concerning formation and movement of such sub-groups. Often nests with other cormorants especially little pied, herons, spoonbills, ibises, and darters.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Assumed to breed annually. Over range as whole, breeding may occur any month, but regional tendencies differ. In New Zealand peaks Oct–Nov and April–May. In N Australia typically summer–autumn but in S Australia spring–summer. At least sometimes dictated by local conditions (dryness and associated state of food in inland nesting areas).

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: (van Tets 1965; Hoogerwerf 1953) Defend by threat, darting head forward whilst gaping and spreading tongue-bone, neck feathers raised and wings partly spread. Male calls harshly whilst female probably silent. Advertising males wing-flick once or twice a sec with usual upward and outward movement of wing-tips. Head rests on back and bill tilted up to $c45^\circ$. Head then swung back and rotated above rump with bill closed. This particular component of display 'gargling', performed by both sexes in context of recognition. Males emit single call as head moves back and double call as it rotates. When female does it, she remains silent. 'Pointing', silent and similar in both sexes, is a pair-interaction; neck stretched obliquely upwards and tail raised to 30° . Pre-take-off characterized by a forward elongated posture with flattened head feathers and raised neck feathers during which throat pulsates with accompanying ticking sound. In post-landing posture head and throat become discoidal, with crest raised and bill closed and pointing down. In 'kink-throating', performed during movement at site, male whistles during early pair-formation and croaks later. Male calls during hopping but female silent.

COPULATION: (GFA)

NEST: Up to 30 m high in tree, over water. Made of sticks, reeds, and other vegetation and oddments like bark and feathers. May be substantial, with deep cup.

EGG/CLUTCH: 49 (44–51) \times 32 (31–33) $n = 12$; 54 (50–56) \times 35 (33–36) $n = 6$; 48 (47–49) \times 32

(31–33) $n = 9$; 47 (45–53) \times 33 (32–42) $n = 40$. Weight: calculated 31.8 g. Clutch apparently 3–6 but modal size variously estimated as 3, 4 or 5; probably 3 or 4.

REPLACEMENT LAYING: No information, but likely to occur.

INCUBATION: Shared; presumably as other cormorants; period not recorded.

CHICK/BROOD: hatchling dark-skinned, becoming clothed in blackish down. Head remains naked with facial skin pale blue-grey and crown purplish. Gular pouch mottled pink and cream. Eye pale brown. Legs and feet blackish. Growth characteristics and behaviour of young not recorded. No details brood.

CARE OF YOUNG: Shared. No details of stints or feeding frequencies. Said to shade young and pour water into chick's open bill.

BEHAVIOUR OF YOUNG: No details.

FLEDGING: No details of behaviour. Period unlikely to be more than $c. 7$ weeks.

POST-FLEDGING: Almost certainly fed, but no information.

HATCHING, FLEDGING, AND BREEDING SUCCESS: No information.

OTHER ASPECTS OF LIFE CYCLE: No information. This cormorant, though common, remains one of least well-researched members of family.

Great Cormorant *Phalacrocorax carbo*

PLATE 6

Pelecanus carbo Linnaeus, 1758, Europe.

Other common names: common, large, large black, European, white-breasted, Atlantic, black cormorant (Australia), black shag (New Zealand), Chinese cormorant, Eurasian, southern. Several perjorative names relating to depredations on fish.

French: grand cormoran. German: kormoran. Spanish: cormoran grande.

Sub-species

P. c. carbo eastern maritime Canada through Greenland, Iceland, and Faroes to Norway and Britain; $c28\%$ of population in Britain and Ireland.

P. c. sinensis probably most numerous sub-species, with huge range: central and southern Europe from Belgium and Holland, E to Baltic and Black sea, also Turkey eastwards across central Asia to Siberia and China and S to India and SE China. Some (c. 5–10% in winter) present in Britain all year. Typically has white head in breeding plumage but some nominate indistinguishable and only safe recognition feature, shape of gular pouch. Later figures on proportions of *carbo/sinensis* therefore highly approximate. Known to hybridize with *P. c. carbo*; some British colonies contain both races (Kirkby *et al.* 1996).

P. c. hanedae Japan. Doubtfully distinct from *sinensis*. *P. c. moroccanus* NW Africa from Morocco to Mauritania; more white on throat and breast than nominate.

P. c. lucidus coastal W and S Africa; inland E Africa; resident Cape Verdes; slighter and can be even whiter than *moroccanus*, but population dimorphic; some dark.

P. c. novaehollandiae Australia, Tasmania, New Zealand, Chatham Islands. Strays to Indonesia and New Guinea. New Zealand population has been separated as *P. c. steadi* (small and dark) but probably unjustifiably.

Description

ADULT M PRE-BREEDING: Overall black plumage glossed purplish, but bronzy on back. Erectile 'mohican' crest of long, white filoplumes extends down back of neck giving variably hoary appearance. Large white patch filamentous feathers on flank. Conspicuous yellow gular skin with white border. Small orange patch below emerald green eye with orbital ring of grey, yellow, or black. Loes yellow to orange. Bill dark becoming yellower at base of mandibles. Legs, feet black.

ADULT F: Similar but often less hoary on head with smaller crest; yellower as against orange eye patch. White thigh patch appears smaller.

POST-NUPTIAL: After laying, hoary head feathers and thigh patch disappear; face dull.

JUVENILE: Vary enormously in extent and pattern of white and dark brown on underparts, from

almost all-dark to all-white posteriorly of a dark pectoral area. Upperparts much like non-breeding adults but less glossy, though gloss detectable. Some juveniles show white speckling on nape and back of neck. Facial and gular skin greenish to lemon yellow, eye grey-brown, eye-ring pale yellow, bill dark, legs and feet black. 2nd winter birds have become glossier and darker beneath though chin and cheeks remain dirty white. Iris becomes green after first year. Mature plumage acquired by year 3 or 4. 3rd winter birds resemble post-breeding adults but still with mottled belly. By following spring similar to adults. White filoplumes and thigh patches may be partially acquired at this stage.

Field characters

Largest cormorant with noticeably stout bill. Adults appear uniformly dark except for face, head, and sometimes neck. Size, bill, powerful flight with slow wing-beats when low and noticeably shallow ones when flying high help to distinguish from European shag. In N America nondescript immatures confusable with double-crested and possibly neotropic but adults of former show less white, more orange gular skin, no white cheek and no crest on nape. Neotropic has some white on chin but markedly smaller with slender bill. In Australasia immature great cormorant may be confused with immature pied but this usually has paler face and sides of neck.

Measurements (see Appendix)

Males significantly larger than females in all dimensions, particularly bill depth and wing length (Koffijberg and van Eerden 1995). No single measurement allows discrimination of sex in >50%; full set allows 90% accuracy (Bauernfeind 1993).

Voice

Highly vocal at colony. Male raucous and louder than female. Inflying male calls 'kok-kok-kok', 'gurr-gurr-rr' with falling intonation and variants during pair interactions; 'ah-aah' associated with hops; a roaring 'roo-roo' post-landing by male and 'phee-ee' by female. Nevertheless even an active colony largely silent and thus quite different from many seabirds (gannet, kittiwake, guillemot). Young

emit continuous thin, whining food-begging calls 'k'ree-kree' or 'kay-yit' and a chirrup audible from afar in calm. A soft warble may be heard.

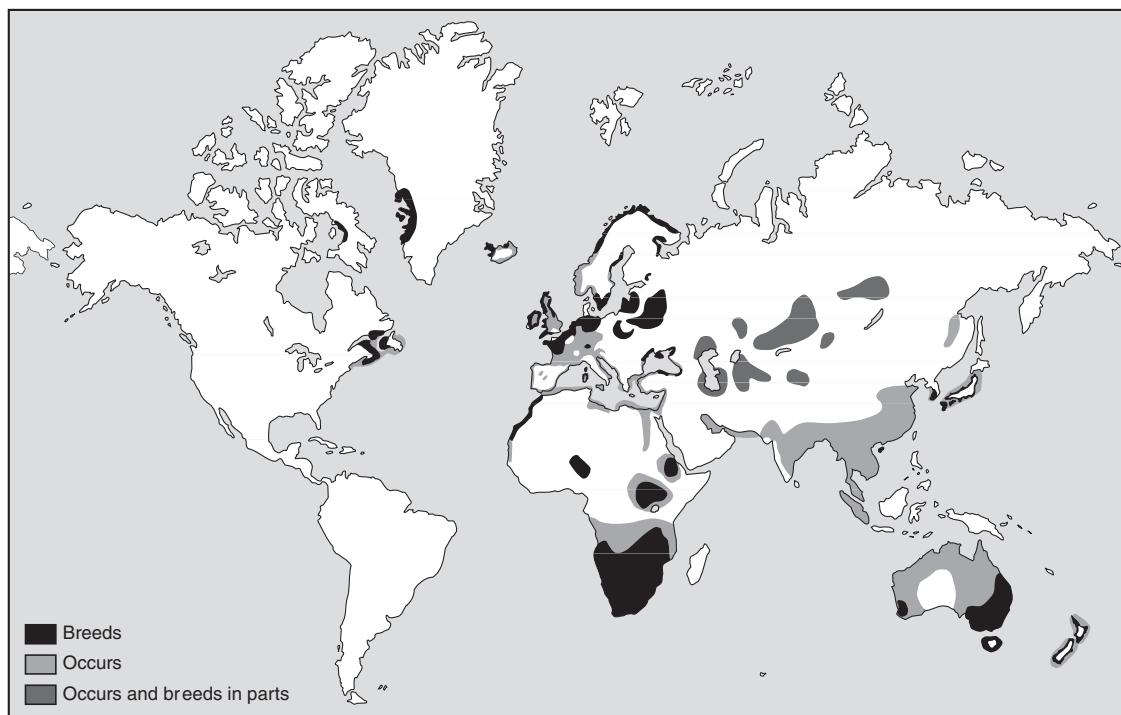
Range and status

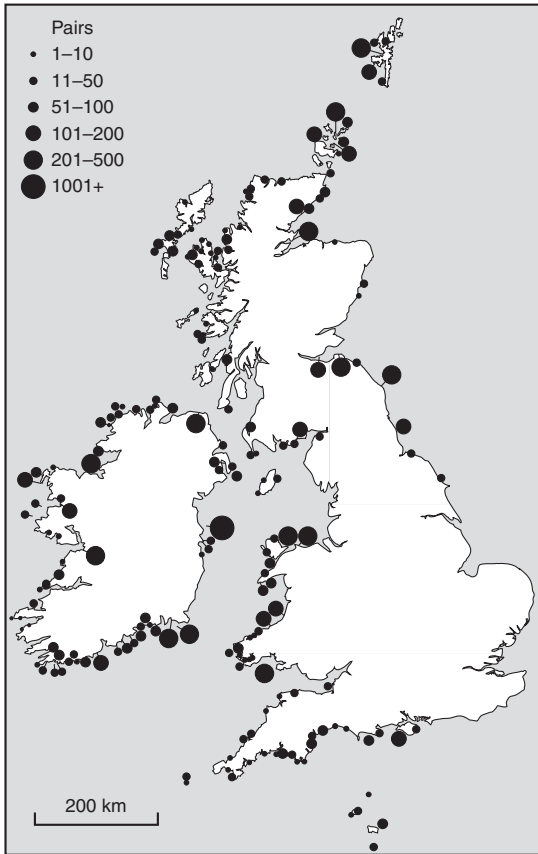
Near-cosmopolitan with wider range than any other pelecaniform; from Iceland to New Zealand through Eurasia and Malaysia, tolerating astonishing range of topography, climate, and habitat from tropical to arctic, sea level to 3,400 m, coast to continental interior, all continents except S America. In Old World occurs mainly between 72°N and 47°S. Straggles to outlying islands and may colonize, e.g. Solomons (Filardi *et al.* 1999).

Despite colossal range, cormorant's numbers relatively modest and far exceeded by even single colonies of several other pelecaniforms. Lacks vast foraging areas open to pelagic species and must usually breed in small, widely dispersed colonies. Competition between this cormorant and European shag may affect distribution but differences in feeding and nesting habits mitigate this. Elsewhere, other

cormorants could compete but given this species' versatility unlikely to limit it.

Impossible to estimate world numbers. Huge but unassessed numbers in Australia (more than 30,000 birds?), 5,000–10,000 in New Zealand and undocumented populations in Africa. For example, a recent (1994) find of more than 10,000 active nests and several big roosts, one of which (on Lake Victoria) held more than 3,000 birds (P. Collins unpublished) suggests many more to be recorded. On Lake Malawi *c.* 10,000 birds (Linn and Campbell 1992). Johnsgard (1993) concludes that status in Canada unchanged in recent years. N America (NE Atlantic coast) holds several thousand (Clapp *et al.* 1982). In Europe, breeding population has expanded everywhere except Hungary. Reviewed by Bregnballe (1996), Trollet (1999). See also van Eerden and Gregersen (1995), van Eerden and Munsterman (1995), van Eerden *et al.* (1995). By mid-20th Century European population small and localized; by 1970s bred in 20 countries, now in 27 and breeding population grown exponentially since beginning 1980s.

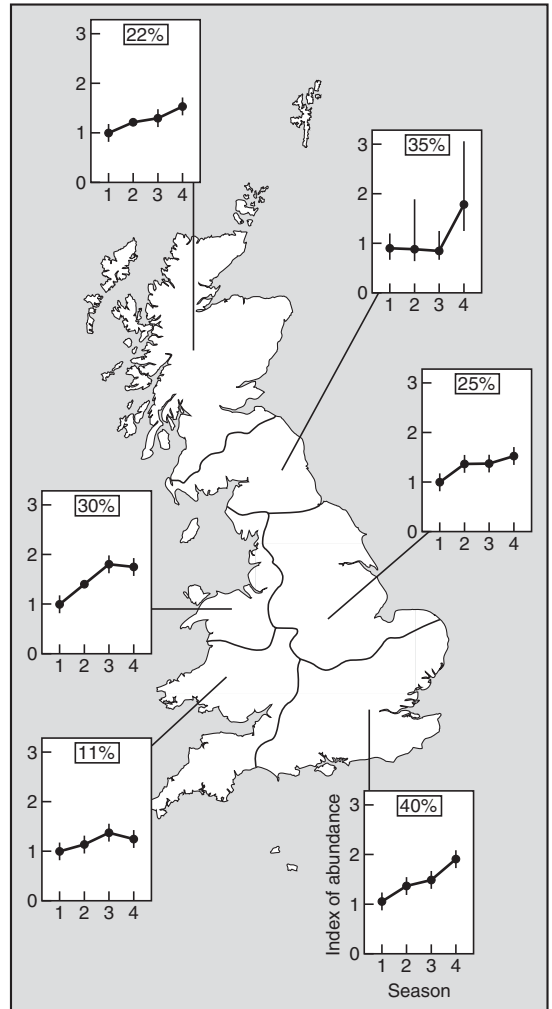




6.107 Distribution and size of British and Irish coastal colonies of the great cormorant (1985–87). (From Lloyd, Tasker and Partridge 1991.)

Now total population >230,000 pairs (180,000 *P.c.sinensis*, 50,000 *P.c.carbo*) (Trolliet 1999). Van Eerden and Gregersen (1995) estimated 60,000+ breeding pairs *P.c.sinensis* in NW Europe; annual increase 16.3% 1978–93. Cranswick *et al.* (1997) gave c40,500 pairs as total European population *P.c.carbo*. W Europe holds c37,000 pairs (Debout *et al.* 1995) of which c. 7,000+ pairs Britain and c. 4,500 pairs Ireland (Kirkby *et al.* 1996). Increase in Britain relatively modest, perhaps <5% p.a. In N and NW Scotland actually declined c20% 1969–87.

For most recent summary of breeding cormorants and shags on N and S shores of Mediterranean to Black and Azov Seas, see Paterson (1994). In Czech Republic numerous enough to cause much conflict with fish-farmers (Mellin 1990); largest colony, in



6.108 Trends in the abundance of the great cormorant in six regions during 4 years (1987–88, season 1, to 1990–91, season 4). Percentage increase over this period also shown. (From Kirkby *et al.* 1995.)

Katy Rybackie, >2000 pairs (1987). In NE Poland 1995 c. 7,000 breeding pairs, an increase of 10% since 1992, new colonies increasing faster than old ones (Mellin *et al.* 1997). In Bohemia and Moravia, since 1987 when killed to reduce population, have recently increased (Janda and Machacek 1990).

Interestingly, prehistoric cormorants in Baltic were nominate race and must have been replaced, as breeders, by *sinensis*. Proportion of *P.c.sinensis* varies widely with country and year—from only 6% in

Denmark in 1971 to 42% in 1991. Immigration to former breeding areas occurred 1982–92. Recent numbers (Bregnballe 1996): England 1,100 pairs (1995); France 950 pairs (1994) (total both races, 3,000, 1995, Trolliet 1999); Latvia 205 pairs (1995); Belarus 850 pairs (1995), total both races *c.* 1,000–200 pairs; Russia 1,400 pairs (1994). Norway recently held 24,000 pairs (Kirkby *et al.* 1996), Denmark 300 pairs, 35 colonies (Bregnballe and Gregersen 1997). Sweden 7,600+ birds, 6 colonies (Olsson 1992) increasing to 15,400 pairs 1995 (Lindell 1997). Holland 1986 5,000 pairs, 1994 *c.* 2,000. Germany 15,000 pairs, 60 colonies by 1995 (Knief 1996). Swiss population increased. Iceland must hold substantial numbers—e.g. nearly 5,000 nests in Faxaflói Bay (Peterson and Ingvarsson 1994). Greenland increased to 2000–3000 pairs, *c.* 110 colonies, 1,000 km coast (Boertmann and Mosbech 1997). Breeding numbers small in Spain, Italy, Greece, and Turkey.

Wintering population in NW Europe 3,900–5,500, central Europe 4,500–5,700, S Europe, Mediterranean, N Africa 81,000–88,000 (*c.* 50,000 Italy) (Van Eerden and Munsterman 1995). Marion (1995) gives wintering population in France (Jan 92) as 66,000 birds, up from 4,000 in 1970. By 1999, 83,000 in 574 roosts (Trolliet 1999). Number wintering in Italy appears to have increased by 400% 1982–86–87 (*c.* 13,000 Martucci and Consiglio 1991).

In winter many continental birds arrive in Britain. Favoured sites such as Morecombe Bay, inner Moray Firth, Lough Neagh/Beg, may hold more than 1,000 birds and many other sites support several hundreds (details in Cranswick *et al.* 1995; summary in Hughes and Sellers 1998). During 1970s–1980s number wintering inland increased in Britain. Of 276 roosts (all types) 72% England, 18% Scotland, 9% Wales and of these, overall, 73% inland (Hughes and Sellers 1998). Between 1987–88 and 1990–91 peak British winter counts of cormorants ranged from 7,966 to 13,866 (Figure 6.108 for roosts). Largest individual count in Nov 1990 gave total British population of at least 18,700, considerably higher than 13,500 estimate for winter 1985–86 (Kirkby *et al.* 1995). As irregular visitor turns up almost anywhere.

For an appraisal of this cormorant as predator and associated conservation problems see Kirkby *et al.*

(1996). In Britain and much of Europe growing pressure from fishing interests for widespread killing. Even been suggested that it may soon become a threatened species here, especially in its freshwater haunts. Several thousands illegally killed every year throughout Britain, especially at Scottish fish-farms. In Ireland, complete protection must be partly responsible for increase of 142% between 1969 and 1987 compared with only 5% in Britain over same period. Disturbed colonies desert wholesale. Calls for a pan-European control strategy (culling) despite absence of evidence that cormorants damage *wild* fish stocks. Callaghan *et al.* (1998) found no overall relationship between density of cormorants and abundance of principal stock fish (rainbow trout) over 167 water bodies.

MOVEMENTS: See van Eerden *et al.* 1995 for discussion; Toms *et al.* 1999 British recoveries; Bregnballe *et al.* 1997 >20,000 Danish recoveries): resident, migratory (or partially) or dispersive (coastally or overland)—*carbo* markedly less migratory (moves less far S) than *sinensis*. May migrate at great height, usually in flocks, 11–40; cross low mountain ranges. In Britain, increasingly overwinters inland in large numbers. About 50% ringed birds recovered within 200 km, *c.* 25% move 200–400 km, remainder go further (Coulson and Brazendale 1968). Adult males stay closest to breeding area, juvenile females migrate furthest S (van Eerden and Munsterman 1995). British and Irish birds highly variable in distance and direction; former generally move S and E, one recovered Tunisia. Birds from SW Scotland may move N or E Britain or to France or Portugal; Galway (Ireland) birds tend to move E across Ireland. North Sea apparently barrier to movement from Britain to Scandinavia; most Norwegian birds moved 400–800 km S. Icelandic cormorants disperse coastally; may enter Baltic. *P. c. sinensis* migrates to Mediterranean and is replaced by wintering birds of nominate race from Norway (Ericson and Hernandez 1997). Winter roosts in W Europe seem to contain more males than females (1:0.66 adults; 1:0.86 juveniles) (van Eerden and Munsterman 1995); may be different mortality rates on migration? Baltic breeders move up to 2,400 km. W European breeders migrate chiefly S to SW, E European S to SE (wide scatter). Move away from Volga delta

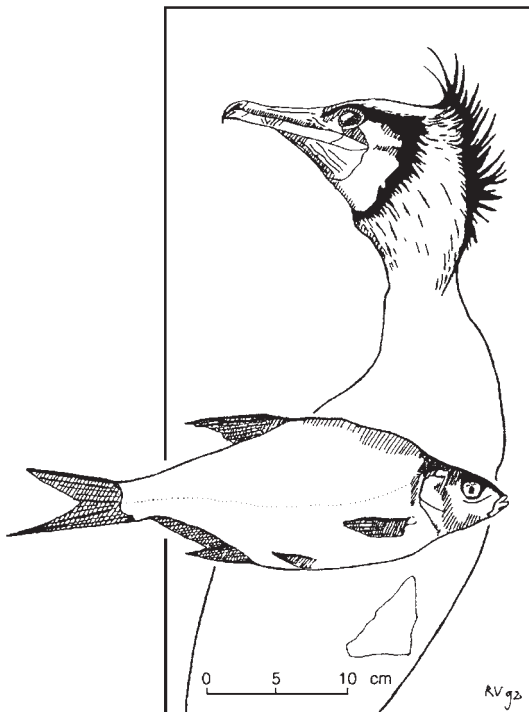
but may over-winter S Caspian. In some areas the breeding population moves out and is replaced by migrants (e.g. birds from Denmark, Holland, E Germany, Poland visit Schleswig-Holstein whilst many local breeders and juveniles move S; Kieckbusch and Koop 1996). Sightings of colour-ringed birds in Switzerland showed that they originated from all parts of the breeding range of *P. c. sinensis*, mostly from Denmark (Reymond and Zuchuat 1995). However Marion (1995) reports in spite of colour-marking 22,600 birds among all European breeding area in 1980s, few proofs of exchange of breeders between countries. Non-breeders anywhere may wander, even in summer. Return in spring may be rapid.

Caution needed in interpreting numbers passing through roosts. In W France most periods spent at roost were <8 days but >21% lasted >3 months (Yesou 1995); number using the roost was 3.9–6.2 times higher than the highest mid-month count. Short stayers tended not to return in consecutive years but long stayers markedly site-faithful (return rate c76% after 2nd winter). Data inconsistent with claim that cormorants nomadic outside breeding season.

Foraging and food

Huge literature; old and new research compared by van Dobben (1995); see also Baccetti and Cherubini (1997).

Breeders forage from near colony to 35 km; 15–20 km not uncommon. Distances vary by colony and day to day; usually 2 or 3+ feeding trips per day. Foraging area of French birds represented only 25% potentially available and individuals used even less (Gremillet *et al.* 1999). Irish birds travelled far to freshwater sites (Warke and Day 1995 suggest some freshwater fish such as roach and perch, predictably exploitable at certain times). Foraging range from roost even greater. Cormorants from two Dutch colonies travelled different distances to same feeding areas; more distant birds made fewer trips but of longer duration. Birds that had to fly further lost weight over breeding season and had consistently lower productivity (Platteeuw and van Eerden 1995). Usually fly out singly but return in skeins (up to 20).



6.109 Cormorant with a bream *Abramis brama* of about the maximum size that can be swallowed. To scale. (From Veldkamp 1995.)

May locate potential prey from air though probably not systematically. May follow conspecifics; detect and prey on pelagics; search for benthics or chance across pelagics whilst diving. Prefer shallow water but can dive to >30 m. Av max dive depth 6.1 m (Gremillet *et al.* 1999). Mean underwater periods 32.6 sec (Scotland), 51 (Canada), 21 (New Zealand), 39.2 (South Africa) (Cooper 1986a). Gremillet *et al.* (1998a) give mean duration 28 ± 21 sec $n = 5,871$, but elsewhere (Gremillet *et al.* 1999) give 40 sec. Longest submergence any race-region 152 sec. These periods much shorter than for many shags, even though shags are smaller. Importance of body insulation for minimizing heat-loss investigated by modelling (Gremillet and Wilson 1999). Lower water temperature and deeper dives drastically increase costs (up to 250%) and may require increased intake of food. Foraging (radio-telemetry) usually once a day, 26–138 min, up to 160 dives per foraging bout.

May feed on foot in few cm, running bill through mud to flush flatfish, or rooting among pebbles.

Essentially a solitary feeder, especially in clear lakes and rivers (de Nie 1995); may nevertheless congregate in thousands. Mass fishing, Lake IJsselmeer, Netherlands, recent phenomenon (van Eerden and Voslamba 1995) coinciding with high numbers of smelt *Osmerus eperlanus* and ruffe *Gymnocephalus cernuus* in turbid water. Social fishing interpreted as adaptation to push small fish from murky water up against light background of clearer top water; in large lake this requires many birds (possibly thousands). At Grober Ploner See social fishing in flocks up to 4,600 birds July–Sept (Koop and Kieckbusch 1997). Has recently become preferred mode in most large eutrophic lakes in post-breeding period; eutrophication favours certain fish species, best caught by communal fishing. Group foraging led to capture of greater biomass, shorter dives but longer foraging periods (Lekuona and Campos 1997a, 1997b). May associate with great white pelican, diving beneath them to catch concentrate.

Diet extremely varied both in range of fish species and size, from fry to fish more than 50 cm. Preferred size in Bohemia 100–200 mm (Musil *et al.* 1995). Flatfish and other bottom-dwellers often predominate; 1–2 year-old flounders *Platichthys flesus* formed 80% of identified prey in Ythan, Scotland (Emerson unpublished). Gremillet *et al.* (1999) found that, off Chausey Islands (France) cormorants fed exclusively on pelagic fish during social fishing (5% of foraging trips) and mainly on benthic prey during other 95%. Took 22 species of fish, 67% benthic. Suter (1997) notes 23 of 31 fish species at a feeding site figured in cormorants' diet but 5–7 species accounted for 85–95% of number of fish taken, mainly roach. Warke and Day (1995) found (Lough Neagh, N Ireland) that cormorants took more marine fish and salmon smolt in years when roach and perch much less abundant. In Greece Goutner *et al.* (1997) found 12 families taken, predominant prey gobies and mullet. Keller (1993) from pellets (Lake Chiemsee, Bavaria) found 22 fish species (59.6% Cyprinids by mass). Prey varied from 30–704 mm, 1–900 g. Keller (1998) found 24 species taken out of 50 found in feeding areas but 89–95% (by numbers) belonged to only 6–10 species, predominantly shoaling fish. Nehls and Gienapp (1997) (Wadden Sea) found prey (13 fish species) mainly yearlings and species-selective

(mainly flatfish). For fish species taken see especially Marchant and Higgins (1990), also Palmer (1962), Rae (1969), Cramp and Simmons (1977), Johnsgard (1993), Keller (1993), Baccetti and Cherubini (1997). Uses full spectrum of prey-size available even in single bout of feeding but not *pro rata*. Nor does commonest fish in diet necessarily represent commonest in feeding area. Brings large items to surface before shaking, tossing, and swallowing. May take eels ashore to eat. Will eat octopus, crustacea, and even young of other waterfowl, but such items unimportant supplement to fish. Probably does not open and eat freshwater mussels as inferred for some cormorant species.

Estimated to eat 14–37% own weight per day in wild; 20% in captivity; 340–520 g. Higher of these figures probably overestimates. Using electronic balances, Gremillet *et al.* (1996) found daily fresh weight of food taken, including that brought to chicks, 890 g (males) and 800 g (females). Elsewhere (Gremillet *et al.* 1995) adult's daily requirement during incubation calculated 238 g, 316 g when rearing young chick and 588 with downy chicks. Voslamber *et al.* (1995) cite c475 g daily intake which they say can be caught in 15 min! (Holland, winter). Dirksen *et al.* (1995b) give mean daily intake 146–699 g with highest values Oct and March. Linn and Campbell (1992) give 250 g daily intake by non-breeding cormorant (Africa) rising to 293 g in breeding season. Keller and Visser (1999) measured daily energy expenditure and calculated cormorant had to eat 341 g fish per day in captivity and 539 g in wild. Stomachs of culled cormorants held 370–720 g of 10 species, mainly roach (Czech Republic, Mellin 1990).

Effects on fish stocks controversial. Staub *et al.* (1998) conclude that winter predation of grayling did deplete older fish leading, to fewer breeders in spring. But Suter (1995a, 1998) found no evidence of negative effects on one trout and two grayling populations even where cormorant densities high. The contrary results arose from the methods of data analysis, as clarified by Staub *et al.* Keller (1995) estimates that at Lake Chiemsee cormorants take 3.3% of total annual fish production, versus 28% by commercial fishermen. Plateeuw *et al.* (1992) for Lake Ketelmeer (Holland) estimated cormorants took c. 11% of standing fish stocks.

Consumption in winter was 8% higher than expected from a daily energy expenditure of $3 \times \text{BMR}$ in summer (probable effect of low temperature). In Denmark, when pounds net-covered, background mortality (rainbow trout) 15% per day. When net removed mortality 98% per day; cormorants emptied pound in c30 min consuming 110 fish weighing c50 kg; took individual fish weighing 1+ kg (Dieperink 1995). On Lakes Veluwemeer and Wolderwijd (Holland) 60% prey commercially valueless ruffe, whilst eel, only species caught commercially, was hardly taken (Dirksen *et al.* 1995b). In 1989–90 total consumption in 2 lakes c. 3.7 kg per ha.

Bite marks on commercial fish may make them unsaleable, but proportion low in Sweden (Engstrom 1998).

Calculations based on pellets somewhat unreliable. Veldkamp (1995), though critical, commends them as giving best results over long-term study, especially if corrected for wear in stomach. Zijlstra and van Eerden (1995), on captives, found pellets (one per day) contained only undigested remains from day before and great variation in proportion of otoliths recovered. Calculating fish mass from otoliths was unreliable.

Cormorants remove some diseased fish from population; in one Polish lagoon, in one year, ate 150 tons ruffe infected with nematodes (Wlasow *et al.* 1998).

Habitat and breeding biology

(See Fig. at end of ch. 5; Kortlandt 1940, 1995; Powlesland and Reese 1999 (breeding phenology, New Zealand); Schjorring *et al.* 2000—long-term study, marked individuals, site choice, fidelity, and breeding success; personal observation)

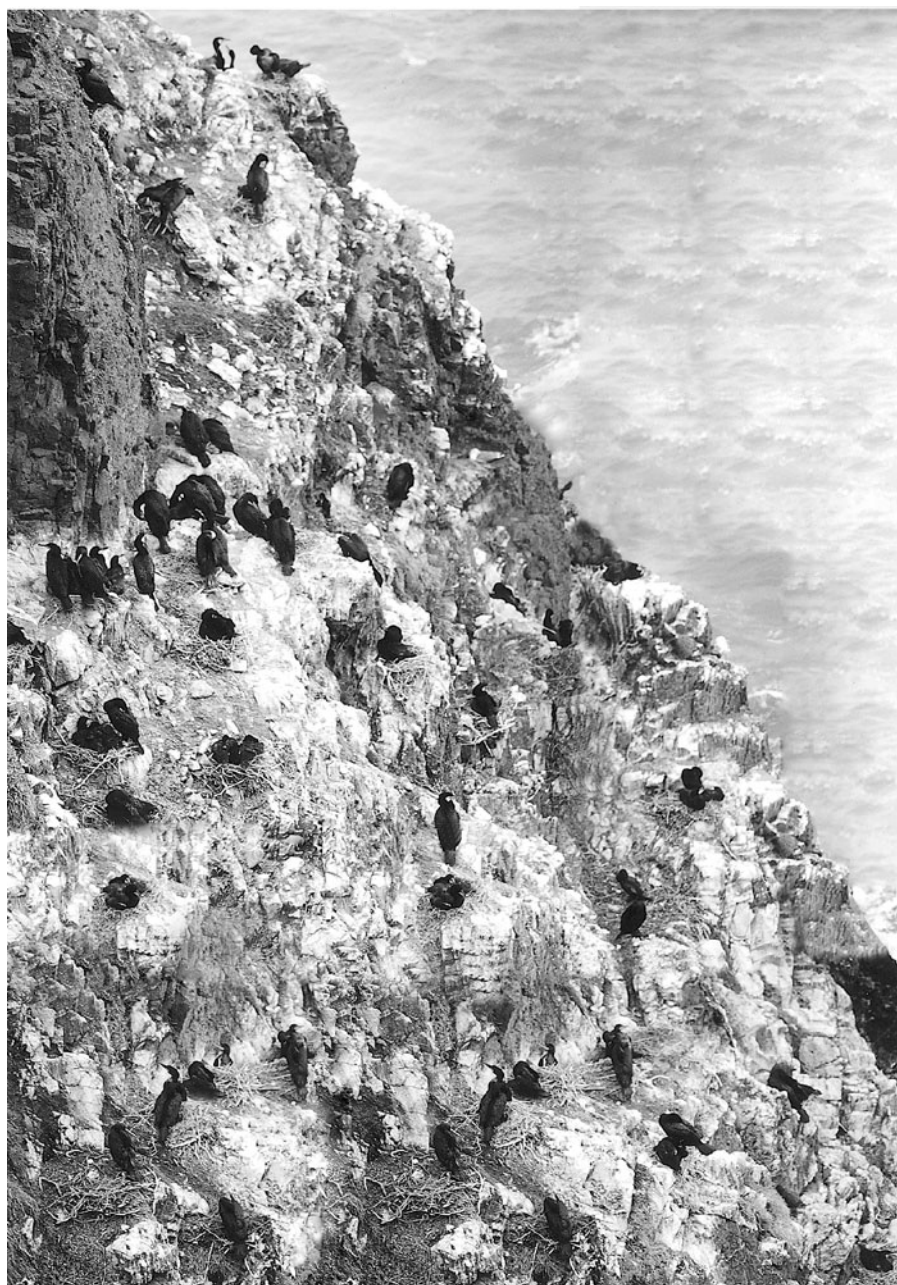
HABITAT: Almost any large area of water, fresh, brackish or saline may attract this cormorant, though tends to avoid heavily overgrown, small, shallow waters. In E Australia almost exclusively on waters larger than 100 ha, many artificial. However, typically coastal, *moroccanus* strictly so and *carbo* very largely in N America. In France, sightings and recoveries marked birds confirms segregation; 80% *carbo* marine, 84% *sinensis* inland (Marion 1995).

Breeding options increased by great catholicity of habitat (cliffs from just above HWM to 100 m, bare rocks, trees, scrub, reeds, artificial, even beaches and sand-dunes). Some colonies ancient but seems typical for nesting groups to change location within a general area from year to year, often returning to vacated area after 2–3 years (personal observation). This habit not contingent on disturbance. Debout (1998) suggests tendency to change breeding location relates mainly to happenings of previous year (Normandy) including disturbance. In Britain has attempted to breed at 35 inland sites (1995 at least 1,200 pairs), significant increase in recent decades, as also tendency to winter inland.

COLONIES: Typically small (10–500 pairs) partly determined by extent of suitable feeding area (water less than 10 m deep within 30 km of colony, Debout *et al.* 1995). Only one colony in Britain and Ireland tops 1,000 pairs, only 3 contain more than 500 and by far most contain fewer than 200 nests, many of them fewer than 50. Smith (1969) notes that in Scotland (c. 3,000 pairs in 41 colonies) only 5 contain more than 200 and largest (Ord of Caithness) held c450 pairs. However, elsewhere, colonies may be considerably larger, e.g. more than 4,000 pairs in Denmark (Ormo colony 4,522 pairs in 1994). Nests tend to occur in discrete groups of unequal size derived from nuclei of displaying males. Adjacent nests may touch but singles, or twos and threes, widely separated, common within colony. Nests often highly exposed even though obviously suffer heat-stress and cormorants not as fond of gloomy caverns as shags. Ease of access seems important. May nest close to other water-birds (herons, ibises, spoonbills, and other members of own family). Although usually not mixed with shags, may nest on same cliff face but at greater height. Often mixes with double-crested in Nova Scotia but largely separated. As with European shag, traffic between colonies, which in some cases increase mainly by immigration. Has been noted that where a major colony has been increasing exponentially, increase in this colony slows down whilst at same time new colonies appear and increase faster than major colony. Many immigrants and first-time breeders involved in these new colonies.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Unlikely that anywhere a given pair breeds successfully more than once per year, though some authors consider double-broodedness likely in areas where laying can occur most months. In

Britain lay mid-March–early July; much variability between regions and years, even between groups in same locality. Peak laying April–May. NE Italy peak laying March with secondary peak May–June. In SE Europe and Russia lays early to mid-April



6.110 Colony (or sub-colony) of great cormorants, Scotland. This cliff is used only intermittently.

onwards; Norway late April to early June peaking mid-May; Bohemia–Moravia April–June; Natal April–Oct; Japan mainly May–June; E Australia July onwards in extensive season perhaps with second peak later and probably nearly continuous in some areas. New Zealand 85% clutches April–May, some June–September; overall mean (1993–98) 24 April. Pre-laying attendance at colony highly variable; some deserted outside breeding period, others used intermittently as roosts. When an extended ‘colony’ consists of several groups as on scattered islets of a skerry, smaller groups tend to breed later (age-composition unknown) but not so in all extended colonies. Because of marked spread of laying in many colonies, fully-grown young adjacent to fresh clutches, season prolonged well beyond 16–20 weeks required by individual pair for complete cycle. Fukuda (1997) analysed lifetime breeding frequencies of great cormorant in Japan 1976–95 (1,838 breeding records involving 468 ringed cormorants of known age and sex). Males $n=246$, aged 1–16 years, bred on av 4.2 ± 3.3 times; females $n=222$ aged 1–17 years, bred 3.6 ± 2.7 times.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Males, either singly or in groups, settle in potential breeding area and begin to advertise for females who may land on fringe or within. Unlike unmated male gannet, who performs ritualized site-ownership display at frequent intervals even without specific external stimulus, male cormorant, though possessing upright, thick-necked posture assumed in aggression-eliciting contexts, does not have equivalent ritualized site-ownership display. Cormorants’ display-sites, many of which eventually become breeding-sites, defended by lunging, grappling, and threat-gaping with aggressive calling ‘croh-croh-croh’ sometimes by fighting, which may be fierce but never prolonged. Kortlandt (1995, comprehensive but individualistic account of courtship) notes that female selects male and that ‘bloody fighting’ may occur between competing females. He asserts that most vigorously displaying male preferred by females but bases this on empirical observations. He ascribes copulation to

‘different’ motivational system than courtship, counter to general view. In sexual advertising display males adopt bizarre posture, standing with head couched backwards between busked wings, breast lowered, bill tilted upwards and tail cocked (Figure 5.33). Tips of folded wings flicked upwards and outwards $c. 1.5$ per sec, tending to cover and uncover white thigh patch in hypnotic fashion, though in side view patch remains visible all time. Males which lack thigh patches display regardless. May wing-flick continuously for up to half-an-hour, sometimes to distant or overflying females. At intervals and without observable change in external stimuli, head thrown back until crown touches base of tail (‘throwback’) when head may be rolled rapidly from side to side accompanied by highly distinctive ‘neighing’ or ‘gargling’ ending in ‘snore’. Thus a rapid ‘ha-ha-ha-ha-GORR-RR’. This part of display, sometimes including throwback, often called ‘gargling’; confusing, since ‘gargling’ is merely vocalization. Typically, throwbacks enter the display, and their tempo increases as a female approaches until occurring about once per 2 sec, balance between wing-flicking and throwback changing in favour of throwback. Often throwback followed by a snake-like upward and forward reaching, usually with gaping bill. Later, male may throwback when alongside female who is on nest and, after pair-formation, either sex, if it is ‘on-site’ partner, performs throwback-with-vocalization when mate arrives. In this situation female’s display less vigorous than male’s. This particular context has caused throwback to be interpreted as a ‘recognition’ display but it should be emphasized that throwback is an integral component of male’s composite sexual advertising display rather than discrete display in own right. As breeding progresses this interaction between partners becomes more and more perfunctory until at change-over on small chicks may be no more than incipient gesture from ‘in-bird’ before it moves off nest. Throwback by an on-site bird may be given as response to potential intruder in which context may be interspersed with attempted jabbing and displacement nest-touching. Nesting adults may give low-intensity throwbacks to dispel encroaching juveniles but full throwback with head-rotation

occurs only in sexual advertising. In incomplete versions, usually in females, bill may merely be pointed upwards or swung slowly backwards whilst gaping and calling loudly, or bird may stretch its neck and wave its head slowly backwards and forwards or from side to side. These neck-swaying variants, comparatively unstructured, probably not discrete displays but indicators of fluctuating motivation.

Before leaving its site, and after it lands, and also when moving to a nearby perch, cormorant assumes distinctive postures and appearances, latter due mainly to alterations in shape of head, which, particularly early in breeding, conspicuously decorated. Take-off preceded by lengthening neck, pointing bill upwards and spreading tongue-bones sideways. May pulsate throat and call 'rrr-rr' and rattle wings briskly. Before landing at its site, inflier gapes widely; males utter loud, gruff 'wow-wow'; female equivalent softer. Depresses tongue bone giving characteristic 'kink-throating'. After landing, conspicuous 'discoidal' appearance produced by greatly enlarging head and throat into laterally flattened disk enhanced by raised median crest; closed bill pointed slightly down. Moving thus, males often 'roar' and females make softer 'puff' sound. These essentially movement-linked behaviours may be performed even when male moves off female's back after mating. Allo-preening (preening partner) sometimes occurs.

Early in pair-formation cormorants have been seen to perform a spectacular presumed courtship flight, mounting vanishingly high before descending with fast glides and banking movements, but not usual.

COPULATION: (GFA)

NEST: Often essential for raising eggs/young above mud and debris in wet weather. Varies from scarcely more than a depression with little nest-material to substantial structure of sticks and debris with lined cup, accretion of years, measuring up to metre across base; cup 20–30 cm. Site is that on which male advertised. Material gathered mainly by male, often communally, pulling vegetation or diving for seaweed. Kordlandt (1995) reports up to 1,000 twigs

brought by male; living twigs not usually used. Nest built mainly by female with sideways building movements, head-quivering etc. Pilfering occurs but without obsessive zeal found in gannets. Material added during incubation and chick-rearing.

EGG/CLUTCH: *P. c. carbo* 66 (58–74) × 41 (38–43) n = 200; calculated weight 58 g. *sinensis* 63 (56–68) × 40 (35–44) n = 250; calculated weight 53. *lucidus* 63 (57–64) × 40 (37–42) n = 6; calculated weight 55. *novaehollandiae* 66 (57–64) × 41 (38–44) n = 100. Clutch 2–5, usually 2–4, mainly 3. Mean clutch sizes: Bohemia 4.15; Norway 3.2 (1983), 3.6 (1984); South Africa 2.54 (but some incomplete); Natal over 2 years 3.05; Quebec 4.4; Australia 4.1. Probably varies with area and year; in new colony Firth of Forth av clutch-size rose by 0.5 egg 1959–61 but much probably depends on age-structure of colony. Smaller clutches characterize first-time breeders. Eggs laid at 2–3-day intervals and first egg at least covered even if not properly incubated. Thus hatching asynchronous.

REPLACEMENT LAYING: Likely if clutch lost; not (?) after loss of young.

INCUBATION: Shared. Webs inserted below eggs. Claim that (presumed) male sometimes feeds sitting mate (in Johnsgard 1993) is unique and needs confirmation, since no pelecaniform known to do so. Change-over involves ritualized pre-landing, post-landing and pre-departure behaviours (above) and the recognition throwback of the on-site bird, often with associated pointing and nest-touching. Usually takes less than a minute and any physical contact is incidental. Relieved male may bring nest-material. During incubation and whilst chicks small, adults probe into bottom of nest presumably removing hard objects. In warm weather will stand off eggs. Incubation period variously given as 27–34 days but 28–30 probably near mean. Shifts last several hours; mean length female (New Zealand) 3 hr 46 min, more than 1 hr longer than male's, but mean absence (foraging) same in both sexes (c. 2.5 hr).

CHICK/BROOD: Hatchling slaty or paler and pinkish on head (bald) with orange-pink gular pouch

which becomes creamy by 2 weeks. Eyes said to be closed for 3 days; seems unusually long. Becomes clothed in dark brownish down by end week 2 though much of head remains bare and pale. Down becomes thick and woolly and wing and tail feathers begin to emerge early in week 4. Fully feathered by week 8 and able to fledge. Eye blue-grey becoming browner, bill pinkish becoming darker, legs and feet pale horn becoming purplish with yellowish-brown webs. At 9–11 weeks voice becomes hoarser and at 11–12 juvenile dissociates itself from nest, disappearing at 12–13 weeks. Body weight and tarsus increased at similar rates and faster than bill or bill-plus-head (Goutner *et al.* 1997). The inflection point in the sigmoidal curves was reached for tarsus, bill, bill-plus-head, and weight on 10, 16, 14 and 19 days respectively. Independent of brood-size and whether hatched 1st, 2nd or 3rd, chicks aged 5–30 days showed weight increases ranging from 56.4–102.8 g per day (Platteeuw *et al.* 1995). These authors give estimates for daily energetic needs of fastest and slowest growing chicks and for total energy needs throughout nestling period. Individual energy needs on av 40% higher in fast-growing chicks compared with slow-growing. Parental fishing effort expressed as total time spent on foraging trips increased with brood-size. To cover max needs, reckoned chick required 632 g per day. Brood 1–4, usually 2 or 3. No obligative brood reduction but young compete for food.

CARE OF YOUNG: Partners share brooding of small chicks, which is constant for at least first 2 weeks. Webs inserted below chicks. Day-attendance may be almost continuous long after close-brooding has ceased. Kortlandt says male takes greatest share of feeding young. Large chicks fed in usual cormorant manner but small ones (less than 2 weeks) said to be fed by direct regurgitation into chick's mouth. Fed at least twice a day, more often when small. A 'small percentage' adults apparently seen to pour water over chick and into its open bill (Palmer 1962). Cramp and Simmons (1977) say chicks perform specific water-begging behaviour and parents bring water in pouch, behaviour shared with pelicans. Said to be deliberately shaded.

BEHAVIOUR OF YOUNG: Once young able to coordinate movements food-begging consists of rapid nodding in vertical plane, sometimes touching adult's bill or gular area, or at a distance, with side-to-side swaying. As chick grows begging becomes very vigorous with rapid pestering and synchronized wing-beating whilst tracking adult's evasive head movements; strong resemblance to booby food-begging. When fully grown, begging becomes violent, with wing-flailing continuing even as food being transferred. Broods of 3 or 4 may engulf parent in sea of beating wings. Variety of vocalizations: when young small, continuous background querulous notes, some with whistling quality, at times almost chirrupy and when young large, rusty 'quing-quing'. When free-flying, young will rush to nest from nearby loafing perch to be fed, and may launch into flight after departing adult, whether fed or not. At 2–4 weeks show quivering movement used in nest-building. Large young defend against intruding adults, head-swaying with repeated horizontal lunges. Will on occasion perform brief and incomplete version of sexual advertising display (wing-flicking). Show marked interest in handling nest-material and may visit neighbouring nests and mildly attack occupants. Little aggression between siblings but nape-biting with facing-away of recipient does occur.

FLEDGING: Fully-feathered young may leave nest for neighbouring area before actually flying at c49–60 days (some accounts put it much earlier but probably disturbed). Av flying age c53 days.

POST-FLEDGING: Fed c30 days, at nest or away from it. In New Zealand, 40–80 days, oldest fledged young seen to be fed 140 days. After variable period most disperse.

BREEDING SUCCESS: Hatched from laid: normally high, 70–80% if undisturbed. Fledged from hatched: 69% (2-year study, Olver and Kuyper 1978) but assessment depends on knowledge of initial and final brood-size, difficult to obtain. Fledged from laid: 63% (n = 15 2-egg clutches); 49% (n = 24 3-egg clutches); 50% (n = 21 4-egg clutches). Fledged per pair: several studies indicate av 1.3–2.5 though figures of 2.9 and 3.1 on record for several areas—e.g. 3.1 (Bohemia and Shetland); 2.89 ± 0.34 , (1990–95, Czech Republic); 2.57–3.42 (overall av 3.03, several

years, large inland colony, France); 2.8 (Italy); 1.7 (New Zealand). Productivity for clutches of different size: 1.2 (2-egg clutches), 1.5 (3-egg clutches), 2 (4-egg clutches) (Olver and Kuyper 1978). Age/experience of adults important in determining both clutch-size and breeding success. Fukuda (1997) found that mean number of fledglings per breeding season for both males and females increased with age for first 6 years but then fluctuated; failure almost entirely due to disturbance and predation on its heels. In Italy, for pairs in immature plumage, 0.26–2.63 $n = 8$. Poor success in Holland (1987–89) partly due to contaminants (Boudewijn and Dirksen 1995).

FIDELITY TO COLONY, SITE, AND MATE: In some regions habitually changes location of colonies which means no possibility of return to nest-site of previous year as focus for reunion of partners. Individuals more likely to return to same breeding site (in the colony) if successful previous season and male site-fidelity was greater than female's. Fidelity to site of both sexes increased with increasing 'familiarity' with breeding area (Schjorring *et al.* 2000). Degree of natal philopatry undetermined but probably partial. Pair-bond described as sustained monogamous but this probably not the rule if 'sustained' means over more than one breeding cycle. Above authors recorded that 92.5% pairs changed partners between years.

AGE OF FIRST BREEDING: Usually 3–5 years (Kortlandt 1940) though breeding at less than 2 years has been recorded. Fukuda (1997) found that in Japan males first bred at 1.7 ± 0.8 years $n = 246$ and females at 2.4 ± 1.01 $n = 222$. In Italy Grieco *et al.*

(1997) recorded 13 pairs breeding in immature plumage, ranging from almost pure white on breast and belly to completely dark brown. Grieco (1999) noted immature-plumaged birds attempting to breed even when nest-sites declined in number (collapse of dead trees) and colony-size had declined.

NON-BREEDING YEARS: Not definitely recorded but Kortlandt mentions apparent loss of condition after breeding in some adults and this species long-lived enough to make it a viable life-strategy. Occurs in European shag, so likely in cormorant.

LONGEVITY AND MORTALITY: Cormorants can live at least 20 years and lifespans much greater than that probable. In northern Azov (western Crimea) max recorded 18 years (Koshelev *et al.* 1997). Adult mortality rates greatly affected by persecution and hence difficult to obtain 'natural' mortality rate. For example, at one Scottish colony nearly half adults may disappear, possibly dead, in one year. In Holland annual mortality for female given as 36% first year, 22% second year, 16% third and 9–14% in subsequent years. Males similar except 7–12% after year 3 (Kortlandt 1942). These estimates, based on ringed birds may be unduly high as consequence of ring-loss. In Azov, birds ringed as chicks lived av 1.9 years; 1st-year mortality 41.2%, 2nd-year 23.7%, 3rd-year 11.2% and beyond that 7.5%. In South Africa Skead (1980) ringed nestlings 1955–73 and 78% of local recoveries were made in first 6 months after ringing, 84% in first 11 months. Of more distant recoveries, 67% in first 11 months. Mean annual mortality rate for this first year of life 55.4%.

Indian Cormorant *Phalacrocorax fuscicollis*

PLATE 6

Phalacrocorax fuscicollis Stephens, 1826, Bengal.

Sometimes placed in *Hypoleucos*.

Other common names: Indian shag.

French: cormoran à con brun, cormoran Indien.

German: Indischer kormoran, braunwangenscharbe. Spanish: cormoran Indio.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Mainly black, with deep blue gloss; scapulars, wing-coverts bronzy with darker edges to feathers giving scaly pattern. Tuft of white filoplumes on sides of head; a few scattered on neck. Eye green, orbital ring green or black, facial skin variously described as pale green, black or purple-black. Bill blackish, gular skin purple black with yellow edge, or yellow all over. Legs, feet black.

F: Similar.

POST-NUPTIAL: Lacks white head plumes, chin whitish, often mottled, overall plumage browner. Facial skin yellowish or brown with yellow marks, gular skin yellow.

JUVENILE AND IMMATURE: Generally brownish above with wing-coverts and scapulars edged darker. Dirty white below; flanks mottled. Eye brown. Upperparts become like adult but underparts generally dark brown with white at bases of feathers.

Field characters

Medium size, long, graduated tail, mainly dark. Pre-breeding adult distinguishable from Javanese, with which overlaps and associates in Indo-Malaysian

area, by white head tufts, absence of erectile crest and green rather than brown eyes (larger size sometimes of doubtful value). Juvenile-immature less-compact 'jizz', larger size, darker bill, proportionately smaller head, more scaly upperparts.

Measurements (see Appendix)

Wing (both sexes): 706 (600–790) n = 5. Weight: c930 g.

Voice

No details.

Range and status

Common and widespread India, Pakistan, Sri Lanka. Also widespread eastwards to southern Indo-China.



6.111 Highly approximate residential range of the Indian cormorant. (After Johnsgard 1993.)

Del Hoyo *et al.* (1992) cite *c.* 6,000 (pairs?) in India, 1,900 Pakistan, *c.* 4,000 Sri Lanka but these figures sure to be approximate and seem too low to justify comment (Johnsgard 1993) 'one of commonest and most widely distributed cormorants of Indian sub-continent'. Local and uncommon in Thailand and Malaya.

MOVEMENTS: Mostly resident. Local movements, extent unspecified, associated with creation and drying up of water bodies.

Foraging and food (Johnsgard 1993)

Often feeds communally, groups (or even just 2 birds) apparently synchronizing dives; no details given. Large feeding flocks may attract terns and pelicans. Winkler (1983) suggests that diet more restricted than smaller Javanese cormorant, which may seem contrary to expectation, but wider than great cormorant's, though cichlids *Etroplus* and *Tilapia* much exploited by all 3, comprising some two-thirds of diet of Indian cormorant. Dives short (av 13 sec), similar to Javanese but only about half as long as great cormorant. Av meal 2.4 fish giving estimated daily consumption of 96 g or 10.3% adult weight. Fish (18 taxa, sizes 30–100 mm) accounted for 90% but tadpoles, molluscs and crustaceans also figure. Of fish, 10 taxa freshwater, 8 brackish. From most-taken to least, fish species: *Mystus* (Bagriidae), *Chela*, *Puntius*, *Catla* and *Labeo* (Cyprinidae), *Channa* (Channidae), *Aplocheilichthys*, *Oryzias* (Cyprinodontidae), *Nantus* (Nantidae), *Anabus* (Anabantidae), *Mugil*, *Rhinomugil* (Mugilidae) and *Platycephalus* (Platycephalidae).

Habitat and breeding biology

(See Fig. at end of ch. 5; although common, ecology and behaviour seems virtually unrecorded)

HABITAT: Another mainly freshwater cormorant, found on islands in rivers and inland waters of various types and sizes and also in mangrove swamps, estuaries, and shallow coastal waters. Mainly low-land but found in higher reaches of some rivers, as in Himalayan foothills. Uses mangrove, bamboo, tamarisk or other, often partly submerged vegetation. Essentially arboreal or, at least, eschews bare ground or rocks. Often associates with Javanese and great cormorant, between which it is intermediate

in size and to some extent in habitat preferences although, often, all 3 may fish same stretch of coast or inland water.

COLONIES: Local populations may be very large, as on Lake Parakrama Samudra in Sri Lanka (peak population nearly 14,000) but colonies never large, often fewer than 50 pairs, amongst other colonial waterbirds.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Unlikely to be more than one successful breeding cycle per year. Apparently breeds mainly during wetter (monsoon) periods in some areas—July–Oct or (Pakistan) on into Dec–Jan, and in cooler period (Nov–Feb) in S India and Sri Lanka. Often unclear whether 'breeding' refers to laying, or being engaged in some stage of breeding cycle. In either case, season obviously prolonged but unlikely to consist of 2 well-separated 'seasons' in same area.

NEST: Sticks and vegetation lined with grass or other suitable plant material. Up to 30 cm basal diameter and *c.* 10 cm deep.

EGG/CLUTCH: $c51 \times 33$. Calculated weight 30.6 g. Clutch 3–5.

REPLACEMENT LAYING: Not recorded but likely to occur.

INCUBATION PERIOD: Unrecorded but likely to be 30 days or less.

CHICK/BROOD: Few details. First down sooty black. Sequence subsequent plumages not recorded. No details about brood or brood reduction, if any.

FLEDGING PERIOD: Not recorded. Likely to be *c.* 7–8 weeks.

POST-FLEDGING: Not recorded.

BREEDING SUCCESS AND OTHER ASPECTS OF LIFE CYCLE: No figures but apparently can be very poor. Other aspects of life cycle apparently not recorded.

Cape Cormorant *Phalacrocorax capensis*

PLATE 6

Pelecanus capensis Sparrman, 1788, Cape of Good Hope.

Now placed by some in *Leucocarbo*.

Other common names: Cape shag.

French: cormoran du Cap. German: kapscharbe, kapkormoran. Spanish: cormoran del cabo.

Sub-species

Monotypic. Shares many ecological characteristics with guanay.

Description

ADULT M PRE-BREEDING: Black, with mainly purplish gloss though bronzy on wing-coverts and scapulars. Scattered white filoplumes on head, neck, vent. Loes feathered. Eye turquoise with bright blue beads on orbital ring. Gape yellow, gular skin orange-yellow. Bill black with basal third bright blue-grey. Legs, feet black.

F: Similar.

POST-NUPTIAL: During incubation or chick-rearing adult loses some white filoplumes, though may retain some on head and neck. Eyes, eyelids pale; gular skin becomes yellow or whitish (sometimes black). Plumage dulls. In winter mostly dull brown with greyish chin, foreneck and upper breast.

JUVENILE AND IMMATURE: Juvenile dark brown on upperparts; whitish cheeks, throat, neck, upper breast. Iris grey, gular skin variably dark, legs, feet brown/black. Immature darkens and acquires green gloss (2nd year?), throat and breast darken and iris becomes bluer. Gular skin pale yellow speckled black and/or white in younger immatures; legs, feet black.

Field characters

Small to medium, sleek, dark, apparently short-tailed marine cormorant with diagnostic yellow-orange

gular area, yellow loes and habit of leaping clear of water before diving. Highly gregarious. May overlap with bank, long-tailed, and crowned cormorants; adult of bank has black facial skin and gular pouch, long-tailed is small with long tail, yellow bill and reddish eye and distinctive patterned appearance on wing-coverts; crowned may be confused more with long-tailed than with Cape. Juvenile Cape pale below whereas bank wholly dull brownish-black (though some individuals leucistic) with black face and gular pouch. Juvenile long-tail has off-white underparts whereas juvenile crowned wholly brown except for pale throat.

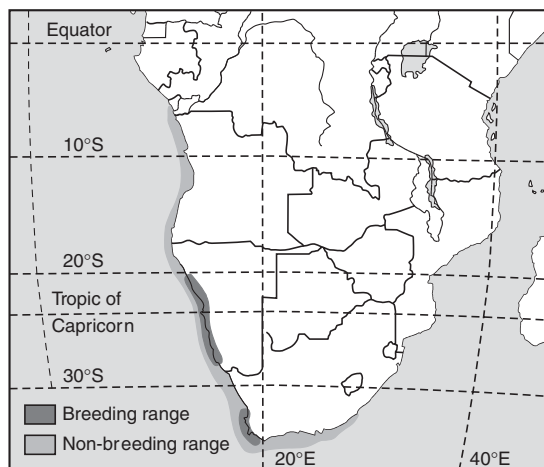
Measurements (see Appendix)

Voice

Croak (both sexes); repeated, low-pitched 'cluck' by male during courtship; 'gra-gra' by male and female; hiss intensifying into explosive bark (threat).

Range and status

Coastal and offshore from Congo river S to tip of Africa and round to Durban on East coast. Most abundant along coast of Namibia (21°41' S–23°20' S) and W coast of South Africa in Benguela current area. Altogether about 15 colonies. Accurate estimates of total South African and Namibian population difficult to obtain. Probable increase since 1956, c. 116,500 birds, to 1978 (372,000). Of 1978 population 112,000 bred on wooden platforms in Namibia in areas with no suitable islands. Seems that Namibian numbers declined 1973–78 related to collapse in pilchards off SW Africa (Crawford and Shelton 1981). Off South Africa, population increased after 1956, on W coast by 50% or more whilst at Dryer Island, only major colony E of Cape Point, numbers increased from c. 3,000 birds in 1956 to more than 46,000 in 1978. Total African population in 1956 c. 1,102,000+ and in 1974 more than a million birds on platforms alone. In 1987 adults (not breeding) present on mainland (Stony Point, Southern Cape). Number



6.112 Distribution of the Cape cormorant. Most numerous 21°45' S to 23°20' S (After Brown, Urban and Newman 1982.)

of Cape cormorants at guano platforms between Cape Cross and Walvis Bay decreased. North of Luderitz feed extensively on pelagic gobies and numbers increased 1978–80. East of Cape Point, too, appear to have increased. Overall, numbers may have increased 1950–73 but certainly declined subsequently (Crawford and Shelton 1981). Causes include changes in food supply, oil pollution (both mineral and fish oil), human disturbance and habitat alteration and adverse conditions such as heavy rain and rough seas. However, difficult bird to census partly because breeding season prolonged but also population never static and counting from aerial photographs involves large potential errors. Some colonies contain large numbers non-breeders (up to 100,000 courting or non-breeding birds on Dassan Island in 1982, Duffy *et al.* 1984b). Of 4 seabirds studied in relation to fish stocks (African gannet, Cape cormorant, African penguin and swift tern) cormorant showed clearest relationship between proportion of population attempting to breed and abundance of anchovies (Crawford and Dyer 1995).

MOVEMENTS: Extensive post-breeding dispersal (max 1,430 km); non-breeding Congo river (NW Africa) to Durban. Often well offshore. Sometimes follows shoals.

Foraging and food

Flies up to 40 km to feeding locations. Often feeds in association with terns, penguins, and gannets. Resembles guanay in feeding in huge numbers, up to thousands, on concentrations of shoaling fish and like guanays, rear birds leap-frog those in front as flock progresses. Dives av c30 sec; feeding bouts (2 per day) tend to be c30 min. Marked difference between feeding ecology of bank and Cape cormorant, former feeding over kelp in littoral zone and making little or no use of shoaling fish which are mainstay of Cape bird which takes smaller prey than bank (Cooper 1985b). Only in inshore waters over a sandy bottom where *Ammodytes* may shoal is there appreciable overlap in feeding ecology. When foraging, Cape cormorants swam faster than bank or great but slower than crowned (Wilson and Wilson 1988). Mean foraging speed along seabed 0.34 m per sec; the deeper the water, the further they travelled over the bottom (see bank for comparative data).

Food principally pilchard *Sardinops* (84% by weight) anchovies *Engraulis* (15% by weight), maas-bankers *Trachurus* and sandeels *Ammodytes*. Anchovies contributed 48%, 97%, 50%, 99%, 30%, 70%, 59% and 60% by mass of prey items in 413 regurgitations collected 1984–92 (Crawford and Dyer 1995). Other species important in some years included sardines (70% in 1988), horse mackerel (24% in 1990), hake (50%, 1984). Fish constitute c91% of diet but takes crabs, lobsters, and a few mussels and squid. Daily intake 133–266 g or 11–22% of body weight.

Habitat and breeding biology

(See Fig. at end of ch. 5; Berry 1976, 1977; Brown *et al.* 1982)

HABITAT: Cliff-edges or ledges, flat inner areas of offshore islands. Will nest on estuarine sand islands, guano platforms, and other artefacts. May nest on tops of bushes up to 3 m.

COLONIES: May be large (up to 120,000 birds). Some competition for space between Cape cormorants, Cape gannets and jackass penguins although somewhat reduced by partitioning of habitat. On flat ground Cape cormorant overlaps significantly

with Cape gannet and the penguin though not with bank cormorant. However Cape gannets and jackass penguins will not use steep habitat which cormorant likes. Max density on flat areas at Lambert's Bay 3.1 nests per m².

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds once a year, so far as known, though more frequent breeding might be possible in some years. Extended laying usually peaks in Austral summer Sep–Feb but in some years birds at some stage of breeding may be found in any month. Apparently largely dependent on state of food supply and breeding liable to be abruptly terminated in adverse circumstances. If spring breeding fails may attempt to nest in following autumn (Crawford and Dyer 1995). As in guanay cormorant, of comparable ecology, birds may emigrate from nesting area after failed breeding attempt. Sep–Feb successive waves of newcomers may establish territories. Williams (1978) says that Lambert's Bay colony composed of apparent residents which start to breed early, on cliff-ledges or islets, and apparently nomadic birds which come in later and nest densely on flat inner areas of island. Thus suggestion (Johnsgard 1993) that this cormorant exhibits sustained monogamy may be wrong. How could permanent bonds be maintained in such a peripatetic species?

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Seems similar to other cormorants. Gape-threat (forward) and rapid head-shaking in withdrawn position accompanied by strikes with bill and various vocalizations. Overt fighting occurs with spread wings and tail and body held low; mainly male–male and involves only bill-grappling. Male throwback occurs from standing or squatting position on presumptive nest-site. Head laid right back, tail cocked and fanned. Display accompanied by low-pitched repetitive call and maintained perhaps for several min. Male does not wing-flick or rotate head but vocalization in throwback position is presumably the 'gargle'. After this, if a female approaches, male repeatedly reaches forwards and upwards up to 10 times in half a min, perhaps with gaping. Presumably, this is 'pointing' and used as

response to approaching female. In her equivalent behaviour, neck arched and vocalizes 'gra-gra-gra'. These recognition interactions may be repeated several times. Once pair formed, male's voice comes to resemble that of female.

Displays associated with landing, hopping, and departure similar to those of other marine shags, 'kink-throat' before landing, long-necked forward position post-landing, gape with head pointing down, neck curved with feathers erected and gular skin prominent during hop. In vicinity of site walks with high-stepping gait and 'S' shaped neck.

COPULATION: (GFA)

NEST: Flimsy; basal diameter c30 cm, cup about half that. Material, mainly dried seaweeds, sticks and flotsam, including plastic, netting and rope, gathered by male either above HWM or by diving. Built mainly by female. Construction said to take c20 hours spread over variable period. Williams (1978) recorded 556 items in one cliff-ledge nest, thus representing a very considerable expenditure of effort, making continuous attendance worthwhile. Pilfering rife. Williams counted c. 1,600 ticks in one nest!

EGG/CLUTCH: 55 (47–61) × 36 (33–38) n = 100; 54 (49–58) × 35 (32–37) n = 110. Weight: 37 (31–42) n = 14. Clutch 1–5, usually 2 or 3. Mean 2.39 n = 1,626 clutches. Laid at intervals of 2 or 3 days. Nests in middle of colonies on flat ground more likely to hold 3 eggs (65%) than those on edge (< 50%), perhaps reflecting greater tendency for edge pairs to be first-time breeders.

REPLACEMENT LAYING: Occurs but no details of replacement period.

INCUBATION: Shared, 22–8 days. Starts with first egg, which takes 28 days; egg 2 c25 days and egg 3 takes 22–3 days. No details on shifts.

CHICK/BROOD: Hatchling black with pinkish undersurface. Within week covered with blackish down except for some white on lower neck, upper breast and leading edge of wing. By 3 weeks feathers appear through down (those of wings, tail, and scapulars) emerging from c. 18 days. Head remains

largely unfeathered. From 26 g (24–31) at hatching, chick increases to 56 (51–64) at 4 days, 234 (190–250) at 9 days, to c. 1,400 g (more than adult weight) at c40 days. Brood usually 2 or 3. Mean brood-size at fledging not recorded.

CARE OF YOUNG: Shared. Apparently may hold wings fully spread with backs to sun, presumably shading young. Other behaviour as normal. Adults leave nest at dawn, returning after about an hour-and-a-half (0.5–3.0 hr) with food. Small young fed 5–6 times per day. Later, adults may make as many as 10 foraging trips per day.

BEHAVIOUR OF YOUNG: May leave nest 5–6 weeks and form small crèches, up to 10 birds. No information on ontogeny of behaviour.

FLEDGING: Can fly at 9 weeks.

POST-FLEDGING: Juveniles fed for several weeks after fledging.

BREEDING SUCCESS: Little quantitative information. Will abandon breeding attempt when food

scarce. In 1985–86 deserted nests at each of 6 major breeding colonies off South Africa and at two biggest colonies off SW Africa. South African desertions for 4th successive breeding season. Conversely, productivity must be high in favourable seasons. On natural sites predation negligible if colony undisturbed. However, large numbers newly-fledged taken by Cape fur seals (2,000+, Dyer Is, summer 1994–winter 1996; or in 1st season c. 7.3% cohort; Marks *et al.* 1997).

FIDELITY TO COLONY, SITE, AND MATE: Fidelity to colony variable. Some birds nest at or close to same site 2 or more years (Berry 1976) but, equally, considerable changes in breeding locations do occur which would make mate fidelity impracticable.

AGE OF FIRST BREEDING: Probably in 3rd year.

NON-BREEDING YEARS: Probable in food-scarce periods.

LONGEVITY AND MORTALITY: Some known to live >9 years. Mortality rates not known.

Socotra Cormorant *Phalacrocorax nigrogularis*

PLATE 6

Phalacrocorax nigrogularis Ogilvie-Grant and Forbes, 1899, Socotra.

Sometimes placed in *Leucocarbo*.

French: cormoran de Socotra. German: Sokotra-kormoran. Spanish: cormoran de Socotra.

Sub-species

Monotypic. Considered to be member of 'guano' shags associated with cold upwellings (Siegel-Causey 1988).

Description

ADULT M PRE-BREEDING: Black all over with usual cormorant green gloss. Purplish on head and scaly effect on back. Tuft of white filoplumes behind eye and scattering on neck and rump. Green eye, black

face and gular skin. Bill blackish with green tinge at base. Legs, feet black.

FEMALE: Similar.

POST-NUPTIAL: Plumage duller. Loses most or all white plumes during breeding.

JUVENILE AND IMMATURE: Juvenile grey-brown above, dirty white below. Feathers of upperparts with blurred pale edges, darker centres. Eye grey, face yellowish, bill dark, legs, feet blackish. During transition to adult plumage underparts become darker brown and there are conspicuous brown blotches on throat and breast. Mantle and scapulars darken, black centres of feathers stand out more. Acquisition of green eye, black face, and gular skin may, it is thought, take more than 2 years.

Field characters

Slim, dark cormorant with noticeably long, thin bill. Smaller and less bulky than great cormorant and adult lacks white edge to gular skin, coloured facial area, and white thigh patch of pre-breeding great cormorant.

Measurements (see Appendix)

Voice

Seems undescribed.

Range and status

Probably now absent from Socotra Island (Gulf of Aden) itself, breeds or has bred on many islands within its limited distribution off Arabian coast, especially in E Persian Gulf. Most recently reported to have declined to 11 extant colonies, from historical minimum of 28, and to world population esti-

mated at between half a million and a million birds (SN 1996). Largest numbers occur from Gulf of Salwa (between Saudi Arabia, Bahrain, and Qatar) in W, to United Arab Emirates in S, and to straits of Hormuz in E (Keijl and Symens 1993). UAE hold 15–33% of world's population. Only colony N of Bahrain suffered serious losses after pollution of 1991 (Gulf War) and reduced to fewer than 20 breeding pairs, but by 1995 had recovered to pre-war level of 100–50 breeding pairs. Gallagher *et al.* (1984) summarizes older records. Recent major colonies cited in del Hoyo *et al.* (1992) and some references in Johnsgard (1993). Include: Zakhnuniyah Island (50,000 pairs in 1980), Huwar Island (50,000–250,000 breeding birds 1981) and Az Zarqua Island (150,000 birds in(?) 1972). Gallagher *et al.* (1984) note some 50,000–250,000 birds nesting in Howar group off Qatar (Oct 1981) and 20,000–30,000 nesting on Zarka (Zirkuh) of UAE. Dec 1987 *c.* 100,000 birds, 1,000 on nests, at Siniyal off UAE coast near Umm al Quwain. Roosts Jazirat Hamar an Nafur (Oman).

Despite these numbers, mostly pre-dating Gulf War, its restricted range, in area of frequent conflict and massive oil pollution, poses real dangers, shown by c25,000–30,000+ birds, mostly cormorants, killed in 1991 oil spill. Sensitivity to man, further reducing productivity, led to classification as 'near-threatened' (Collar and Andrew 1988, Symens *et al.* 1993). Johnsgard (1993) cites localities affected by oil, etc.

MOVEMENTS: Disperse post-breeding (Persian Gulf, Arabian Sea). Vagrant Red Sea (Somalia, Ethiopia), W India (del Hoyo *et al.* 1992). Feeding movements.



6.113 Distribution of the Socotra cormorant. (After Johnsgard 1993.)

Foraging and food

As with guany and Cape cormorants, foraging flocks often contain many 'aerial scanners'—large groups flying low and often entering water from air in 'plunge dive'. Flock-feeding seems communal rather than cooperative. Within its range there are strong currents and areas of cool, enriched water. Dec–Feb (cool season) off Somalian coast may be enormous concentrations of small fish exploited by seabirds, including Socotra cormorant. 'Quite the most

spectacular sight, again in the cold weather, was the big flocks of Socotra cormorants swimming close inshore in big rafts (estimated 6000)' (Bailey 1971). Keijl and Symens (1993) report that in spring, summer, and autumn, flocks numbering from a few to several thousand can be seen from N Arabian shores.

Submergences lengthy (1–3 min) in water 6–10 m deep. No details of prey.

Habitat and breeding biology

(See Fig. at end of ch. 5, Johnsgard 1993)

HABITAT: Exclusively marine-coastal within range of productive upwellings, as off Arabian and Somalian coasts. Typical habitat bare coastal cliffs and islets (possibly persecution some effect); vegetation usually sparse or absent.

COLONIES: Although Johnsgard cites colonies of several thousands, up to 250,000 pairs, these may no longer exist and colonies usually a mere 50–100 pairs. Where large colonies do exist, density may rise to 4–6 nests per m² (comparable to densest guanay colonies) but often much sparser.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Annual breeder; said to nest mainly

summer in Persian Gulf and winter off SE Arabia. Keijl and Symens (1993) give Sep–Mar as breeding season in Arabian Gulf. Laying may occur outside these periods. On Kuria Murias breeds Jun–Oct and off Saudi Arabia eggs noted in Apr, May, Sep, Nov and Dec. On Halne Island, Persian Gulf, lays Jan–Mar. Laying may well be affected by inconstant availability of food over its range.

No details of breeding behaviour. Display needs studying.

NEST: Simple scrape in sand or gravel or among boulders.

EGG/CLUTCH: 57 (56–9) × 39 (38–41) n = 6. Calculated weight 48 g. Unusually for cormorant, eggs said to have dark brown spots and blotches at one end. Clutch usually 2 or 3, sometimes 4.

CHICK/BROOD: Nestling (age unspecified) covered with pale down. Face, gular pouch and bill pinkish, eye dark, legs and feet pale nondescript. No details of development or brood.

BREEDING SUCCESS AND OTHER ASPECTS OF LIFE CYCLE: No details.

Bank Cormorant *Phalacrocorax neglectus*

PLATE 6

Graculus neglectus Wahlberg, 1855, SW Africa.

Now referred to by some as *Compsohalieu*s.

French: cormoran des bancs. German: kusten-scharbe. Spanish: cormoran de bajco.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Almost uniformly dark; black with green-bronze sheen in new plumage, brown when faded. Long white filoplumes on rump and small ones on forehead and neck.

Feathers of mid-back, wing-coverts and scapulars round-tipped, bronzy, with black margins. Flight feathers and tail blackish. Short erectile crest on forehead. Eye orange-brown (top half) and greenish tending to blue (bottom half). Orbital ring black; mouth and gular skin black; bill black with lighter tip; legs and feet black.

F: Similar.

POST-NUPTIAL: White filaments on rump, head, and neck lost during incubation, body plumage fades.

JUVENILE AND IMMATURE: Completely dull. Dark brown to black with brown eye tinged bluish.

Immature similar to dull, unadorned adult but some 2nd-year birds acquire some white filoplumes though full adult plumage not acquired until 3rd year. Iris from greenish (2nd year) to fully-adult bi-colour in 3rd year, when first breeds.

Field characters

Large, dark, corpulent marine cormorant, often with noticeable eyes appearing yellow. Early in breeding season adult's white filoplumes diagnostic. Limited to coast of SW Africa. Not-uncommon leucistic individuals with varying amounts of white on face and neck differ at all ages from other South African cormorants in blackish facial skin and gular pouch.

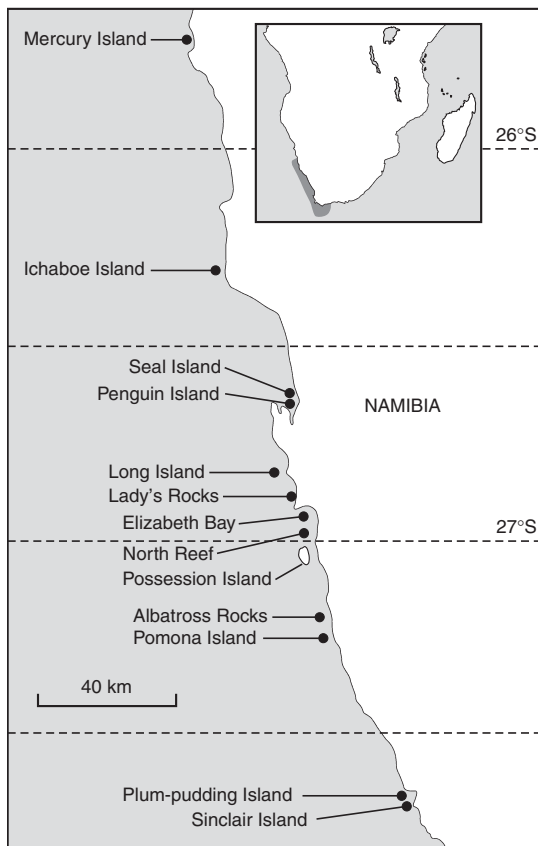
Measurements (see Appendix)

Voice

Described only as 'croak'.

Range and status

Endemic to coastal SW Africa (Benguela Current) from 120 km N of Walvis Bay S to Cape Agulhas. Breeds from Hollamsbird Island (Namibia) to Quoin Rock (South Africa) (Cooper 1981), although Williams (1987) saw birds in breeding plumage, manipulating nest-material just S of Swakopmund, 150 km N of Hollamsbird Island, and thus well outside recorded breeding range. c44 breeding localities containing c. 18,000 adults mainly (71%) on Ichaboe and Mercury Islands, largest colony containing c. 2,600 birds. Although total population small, future perhaps safe if breeding birds protected from disturbance and thus from predation by kelp gulls. In fact population increased after 1956, possibly benefiting from good supply of pelagic gobies. But Cooper suggests expansion of fishing may affect large populations of Ichaboe and Mercury, and Crawford *et al.* (1999) report disturbance resulted in loss of 4 colonies and reduced populations at 6 others. Ichaboe and Mercury lost c. 3,000 pairs (latter through Cape fur seals) in 1980s and reduction in food (1990s). Overall breeding pairs fell from 8,672 (1978–80) to 4,888 (1995–97). Present status thus 'vulnerable'.



6.114 Bank cormorant breeding localities off SW Africa/Namibia. Non-breeding range extends N and S of this (see text). (After Cooper 1981.)

MOVEMENTS: Strongly sedentary but movements of juveniles up to 459 km (av 153 n = 4). 86% adult recoveries <10 km of where ringed; max 168 km (Cooper 1981).

Foraging and food (Cooper 1985b, 1985c)

Birds fly to feeding areas from roost or colony, in small groups. Does not forage in exceptionally rough seas. As an inshore marine cormorant it typically forages at max 8–9 km from shore, either singly or in small loose groups, individuals of which feed independently. Usually avoids even estuaries although Williams has seen them among Cape and great cormorants at mouth of Swakop River, though feeding ecology differs from these

two species. Breeding males foraged for 3.47 bouts per day and females 3.02 bouts, but total time spent foraging much the same. Difference speculatively related to sexual dimorphism (males larger than females). Duration (mean) of foraging bouts 84.3 min in breeding females but only 68.4 min in males. Feeds mainly on bottom where ground rocky, or over coarse sand or shingle, often covered with kelp; may dive at least 28 m deep. Wilson and Wilson's (1988) study of diving behaviour of this species comparing sympatric Cape, crowned, and great cormorants showed that, like Cape, it dived at an angle of $c60^\circ$ to surface. Vertical descent speed, at 0.69 m per sec, slower than others. Swimming speed whilst diving 0.8 m per sec and foraging speed along bottom 1.45 m per sec. Latter faster than others but, as in other 3, highly variable, presumably depending much on nature of seabed. During comparatively long submergences av 45 sec (max 63.8) birds search crevices for bottom-dwelling fish and crustacea, often travelling many metres. 21% of prey by mass consists of invertebrates, mainly lobster, crab and octopus. Of remaining 79%, fish associated with kelp made up 61% (mainly blennies and klip fish), 12% mainly bottom dwellers and only 1% pelagic shoalers. But away from kelp beds feeds more extensively on mid-water fish. Near Ichaboe and Mercury Island fed very largely on pelagic gobies. Thus hardly competes with Cape cormorant, main relative in area.

Habitat and breeding biology

(Little known) (See Fig. at end of ch. 5; Cooper 1987 (particularly clutch-size; cf well-studied European and South Georgian shags)

HABITAT: Breeds on rocky, windy and often spray-swept pinnacles or rocky offshore islands where nests close to sea; sometimes washed away. Reputedly habitat limited by heavy build and difficulty in taking off. Will use artificial structures.

COLONIES: Usually <100 pairs; compact.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually though thought occasionally to raise 2 broods in one year (see Ryan and Hunter 1985). May lay in any month. At

Robben and Malgas Islands (W South Africa) main breeding season May–Oct; Ichaboe and Mercury (central Namibia) mostly Nov–May (Crawford *et al.* 1999). Beginning to build to laying *c.* 1 month (Cooper 1986b).

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: No details of territorial behaviour. Performs version of typical male advertising display. Throwback takes head backwards until it touches the back, bill pointing vertically upwards. Then head sweeps forward and down, in a bow. Alternate backward and forward movement said to cover and expose white area on rump. Nothing said about wing movements. Other ritualized behaviours common to cormorants not mentioned though versions of them are certain to occur. After pair-formation female guards nest.

COPULATION: No details.

NEST: Large or very large (up to 6 kg). Uses mainly filamentous green seaweed for which it dives (also sticks, feathers). Wet algae adheres well to smooth, often sloping rock on which it nests and excreta helps cement it. Male brings nest material throughout breeding cycle. Opportunistic pilfering from neighbours' nests. Williams (1978) found no ticks in bank cormorant nests; hundreds in Cape's.

EGG/CLUTCH: (Cooper 1987): 59 (50–67.1) \times 38.4 (31.3–42.1) $n=575$. Weight: 50.4 (44–69) $n=87$; *c.* 2.8% female weight. Varies with position in clutch. Mean volume (estimated) 44.4 ml $n=475$. Shell thickness, including chalk layer, 0.27 mm (0.25–0.29) $n=5$ in egg 1 of 2-egg clutch; 0.34 (0.31–0.38) $n=5$ in egg 2, a highly significant difference. Shells thicker in some parts than in others. In 6 other cormorant species shell thickness varies between 0.28 and 0.44 mm so bank cormorants are not unusually thick-shelled.

Although eggs of 1-egg and 2-egg clutches not significantly different in size, those of 3-egg clutches smaller. Within clutches, dimensions and fresh-egg mass decreased with order of laying in

clutches of 2 and 3 but only significant difference that between egg 1 and egg 3. Similar variation in egg-size with order of laying found in several cormorants (see *P. atriceps*, *P. coronatus* and *P. aris-totelis*).

Seasonal variation in size (estimated volume and mass) also followed predictable pattern; biggest eggs in mid-season, smallest late in season.

Seems to be only adequately studied cormorant species which 'never' lays more than 3 eggs. Mean clutch-size 2.02 $n=252$, with 1-egg clutches comprising 15.9% of sample, 2-eggs 65.9% and 3-eggs 18.2%. Yet eggs not appreciably larger, as proportion of female mass, than those of other species (mean fresh clutch mass equals 5.7% of female mass compared with 4.7–16.6% for other species). Cooper (1987) could not detect seasonal trend in clutch-size but perhaps masked by small sample. Mean laying interval 3 days (max 9 days); between egg 1 and egg 2, 2.7 days in both 2 and 3-egg clutches. Between egg 2 and egg 3 it was 4.3 days (av laying interval in cormorants 2–3 days).

REPLACEMENT LAYING: Replaces lost clutches but does not make part-lost clutches up to full size. Thus a determinant layer, as most cormorants appear to be (observation of Potts *et al.* 1980, that European shag quickly replaces eggs lost during laying, up to max of 9 eggs, remains to be explained). Size of replacement clutches similar to first clutches. Mean interval between laying of first clutch (full?) and replacement clutch (full?) 79 ± 51 days (24–161) $n=7$. At one nest, 3 clutches initiated in one 'season' (unspecified) though whether known to be by same female not stated. Will re-lay after lost broods as well as after lost clutches. Re-laying interval increases as season progresses. From his data, which are highly variable, Cooper concludes that bank cormorants require at least 23 days to begin new clutch, same as min time required between beginning of nest-building and commencement of egg-laying. Comparatively long interval required by bank cormorant compared with

European shag may be related to much shorter breeding season of latter.

INCUBATION: Shared about equally, changing over during daylight hours. Off-duty bird usually roosts alongside nest. Eggs never normally unattended. Shells removed but unbroken infertile eggs may remain in nest. Apparently often displaces eggs during incubation and these may be found alongside nest.

Eggs hatch asynchronously in order in which laid, mean hatching interval 2.7 ± 0.5 days. Laying interval between egg 1 and egg 3 greater than their hatching interval presumably because full incubation did not begin with first egg. In 2-egg clutches egg 1 hatched in 29.5 ± 0.5 days (29–30) $n=8$ and egg 2 hatched in almost precisely the same amount of time. In 3-egg clutches egg 1 hatched in 31 days $n=1$, egg 2 in 29.7 (29–31) $n=3$, egg 3 in 28.8 ± 2.6 (25–31) $n=4$.

CHICK/BROOD: Hatching takes 1.2 ± 0.4 days. 'Pipping' always occurred near blunt end. Chick sooty black with some white down on head, neck, rump and wings. Usually only 1 or 2 chicks by end of period in nest.

CARE OF YOUNG: Shared. No unusual details.

BEHAVIOUR OF YOUNG: No details.

FLEDGING: Young leave nest when fully grown except wings shorter than adults' and unable to fly properly. No details of fledging period.

POST-FLEDGING: Apparently young fed for up to 3 months after fledging, but young said to leave nest before they can fly properly.

BREEDING SUCCESS: Seems no details. Highly sensitive to disturbance; may lose eggs and young to kelp gulls.

OTHER ASPECTS OF LIFE CYCLE: Seems no details. Thought not to breed before 3rd year.

Japanese Cormorant *Phalacrocorax capillatus*

PLATE 6

Carbo capillatus Temminck and Schlegel, 1850, Japan.

Synonymous with *P. filamentosus*. May form super-species with *P. carbo*.

Other common names: Temminck's cormorant, sea cormorant, Ussurian cormorant. French: cormoran de Temminck. German: Japankormoran. Spanish: cormoran Japone's. Japanese: umi-u.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Closely resembles great cormorant but some individuals have dense, ragged white beard of filoplumes sprouting from bottom edge of extensive white gular facial skin (lacks yellow edge of great cormorant's gular skin) and extending round to sides of upper neck. Also white filoplumes on forehead, crown and nape. White thigh patch.

F: Similar but 26% lighter than male.

POST-NUPTIAL: Loses hoary head plumes, facial colours become dull, chin and throat become pale and plumage generally less glossy-green.

JUVENILE AND IMMATURE: Juvenile various shades of dull brown above and brown-tinged white below with larger blotches on flanks. Bill dingy yellow. Gives rise to out-of-breeding adult plumage by darkening of underparts whilst upperparts become green-glossed black. Colours of soft-parts develop in 3rd year.

Field characters

Adult may be distinguishable from great cormorant by greener wing-coverts (not too reliable), 'beard' (pre-breeding), absence of yellow border to gular skin. Juveniles not certainly distinguishable because great cormorant so variable; Japanese said to be

browner with yellower bill. Some immatures, likewise, may be indistinguishable. All ages Japanese more marine than great where they overlap.

Measurements (see Appendix)

Voice

As *P. carbo*.

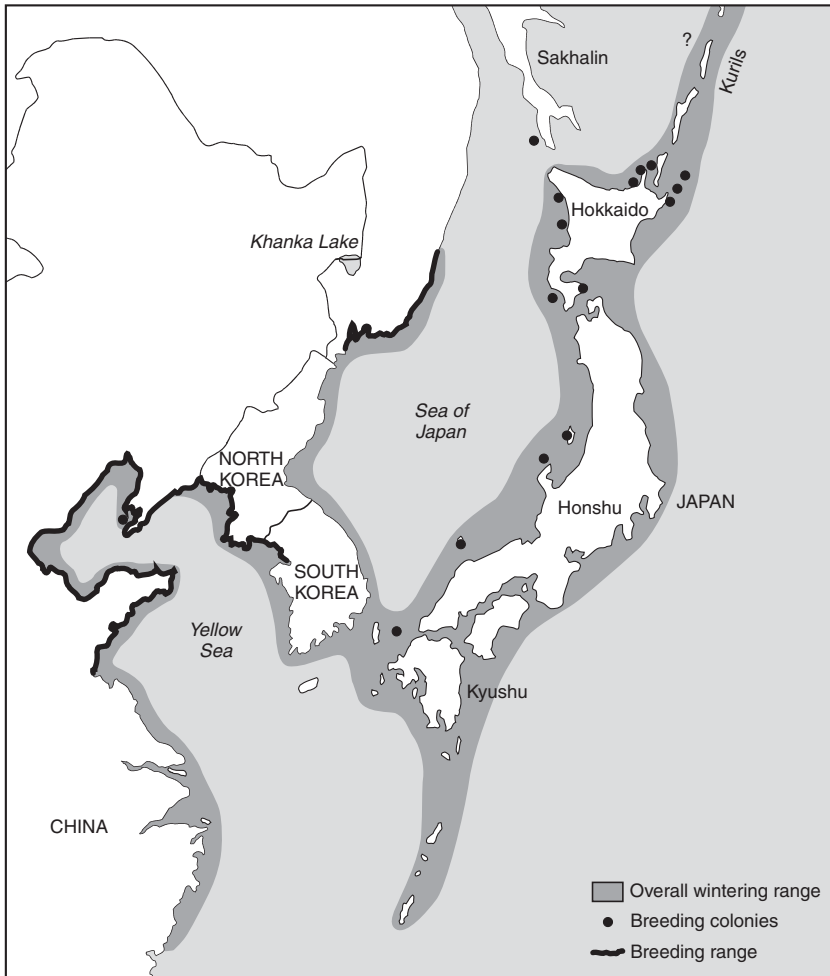
Range and status (del Hoyo *et al.* 1992)

Essentially cormorant of rocky coasts of central and northern Japan from Kyushu (where may no longer breed) north to Sakhalin Island and in southern Kuril Islands. Breeds, also, on coasts of China, Korea, and southern Siberia. Hokkaido (Japan) held *c.* 1,900 pairs in 1980s. Other census figures: 825 South Korea 1990; fewer than 16,000 birds former USSR (SE Siberia), *c.* 7,000 on Kuril Islands, 5,000 along mainland coast of Sea of Japan and 3,000 in Peter the Great Bay. Largest known colony on Furugelm Island (1,500 birds in 1985). Intense persecution by man in 1940s–1950s devastated all accessible colonies on Sakhalin and southern Kurils (del Hoyo *et al.* 1992). Introduced arctic foxes have ravaged some colonies in past. However, Hokkaido population considered to have increased during 1970s. Some 20 colonies on west coast of Shiretoko Peninsula fluctuated considerably between 1979 and 1985 though, overall, numbers did not change much (Watanuki *et al.* 1988). Closely related to great cormorant and although both species occur in Japan their distribution apparently shows little (any?) overlap.

MOVEMENTS: little information; post-breeding disperses relatively short distances.

Foraging and food

Johnsgard (1993) details behaviour as captive fisherman. Watanuki *et al.* (1996) found male dives av 15.1 m, lasting 37 sec, female 7.2, 24 sec. Females spent similar proportion of time as males searching the bottom and, over a day, spent as much time underwater.



6.115 Distribution of the Japanese cormorant. (After Johnsgard 1993.)

They dived and ascended as rapidly as males. In neither did longer submergences lead to longer post-diving recovery times. Kato *et al.* (1998) showed (2 birds, male and female) that they foraged within 5 km of nesting island, between it and mainland, apparently in water 10–60 m deep over rock and sand. Both were faithful to their own foraging area and depth.

Habitat and breeding biology

(See Fig. at end of ch. 5 del Hoyo *et al.* 1992)

HABITAT: Gregarious marine cormorant of rocky coasts and islands sometimes with red-faced

cormorant but using different nesting habitat. Rather than cliff-ledges prefers flat, cliff-top areas, rocks, and islets. Unlike great cormorant seems not to nest in trees or on precipitous cliffs.

COLONIES: Largest contain several hundred pairs (Japan).

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually. Lays early May through to (at latest) mid-July off eastern Hokkaido. Probably most eggs laid 2nd half May. Elsewhere laying may be slightly later but still largely within these dates.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Displays not documented but likely to be similar to great cormorant.

NEST: Often only insubstantial, probably due to lack of readily accessible material. Takes *c.* 10 days to build; material collected from vicinity of nest by male.

EGG/CLUTCH: $c62 \times 40$ mm. Calculated weight 54.75 g. Clutch probably usually 3 (which is often initial brood-size).

REPLACEMENT LAYING: Occurs.

INCUBATION: Shared. Yamamoto (1967) reports one partner (male?) feeding other. Major departure from pelecaniform behaviour if more than aberrant instance. Incubation period estimated *c.* 34 days but probably much as in great cormorant.

CHICK/BROOD: Few details. First downy plumage blackish, later becoming whitish below. By *c.* 4 weeks uniformly dark brown down with bare, whitish head and yellow gular skin. No information on scale and method of brood reduction, if any, nor of interactions between young, but mean brood-size 2.5, so little reduction.

CARE OF YOUNG: Between them, young seen to receive 7 apparent feeds in little more than an hour.

Generally, each adult foraged *c.* 5 times a day with peak activity morning and evening. Chicks brooded in shifts of 2.5–3 hr. Adults occasionally regurgitated water but so haphazardly that usually missed chick for whom, presumably, intended. Nevertheless Yamamoto (1967) saw parents return with water and disgorge it, 4 times at 5 min intervals. As with shading, this potentially important activity seems ill-oriented, unsystematic, and poorly differentiated.

BEHAVIOUR OF YOUNG: No details but likely to resemble great cormorant. Flattish sites may facilitate crèching, since chicks leave nest *c*40 days.

FLEDGING: No description but likely to be gradual increase in wing-exercise and short flights. Begin to leave nest *c*40 days. No details about age of first sustained flight but unlikely to be less than 7–8 weeks.

POST-FLEDGING: Fed but no details.

BREEDING SUCCESS: Johnsgard (1993) cites minimum av brood-size of 2.5 young in 71 nests; those on isolated rocks av 2.8 and on cliff-tops 2.4, possibly because latter younger birds occupying less favourable sites. At a different colony av brood-size (large young) 1.9 (9 with 1 chick, 7 with 2 and 6 with 3).

OTHER ASPECTS OF LIFE CYCLE: No details. Unlikely that mortality rates and longevity differ much from great cormorant.

Brandt's Cormorant *Phalacrocorax penicillatus*

PLATE 7

Carbo penicillatus Brandt, 1837, no locality.

Sometimes put in genus *Compsohalieu*.

Other common names: brown, pencilled, Townsend's, tufted cormorant.

French: cormoran de Brandt. German: pinselkormoran, pinselscharbe. Spanish: cormoran sargento.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Moderately large, dark cormorant with slender bill and high forehead. Head and neck glossed purplish and back, rump and underparts glossed greenish. Tail and outer vanes of primaries bronzed. Secondaries and inner vanes of primaries brownish. Whitish filamentous plumes *c*60 mm behind ears and on neck and scapular area. Vivid, cobalt-blue face and blue pouch bordered by yellowish. Mouth lining blue. Eye green or blue. Bill dark. Legs, feet black.

ADULT F: Similar but duller.

POST-NUPTIAL: During incubation filoplumes disappear, gloss dulls, facial and gular skin turn slaty.

JUVENILE AND IMMATURE: Juvenile mostly brownish-black, paler on underparts, especially chin; feathers around greyish gular area light grey or brown. Feathers of scapulars and wing-coverts distinctly margined light brown and often light-coloured 'V'-shaped pectoral band. Eye dark blue-grey or brown, and face brown or purplish. Bill dark and legs and feet blackish. Juvenile plumage gives way to basic adult pattern though young adults may breed before full panoply of plumes acquired.

Field characters

Moderate-sized cormorant with slender bill, rather high forehead, comparatively short and rounded tail. Distinguishable by band of pale yellowish feathers bordering gular area. Juvenile underparts darker than double-crested and already shows pale border to gular area. Immature not as dark as pelagic cormorant, shows more buff on ventral surface, especially upper breast ('V' or 'Y' pattern).

Measurements (see Appendix)

Voice

Characteristically cormorant-like croak or growl; incisive 'kauk' repeated about once per sec, often when swimming; loud, hoarse gargle in display. No sex difference mentioned. Williams (1978) remarks particularly on absence of vocalizations from advertising birds and general lack of voice compared with some cormorants.

Range and status

Pacific coast North America from British Columbia to Baja California and on islands off Baja and in Gulf of California. Recently local in SE Alaska mainly on Juneau Peninsula. Alaskan, British Columbian and Washington populations small and recent. BC population declined from *c.* 150 to 50 (1970–82). Further S, in Oregon, Brandt's is dominant species; *c.* 16,000 birds in late 1970s. In California, where *c.* 75% of world's population nests

(64,000 breeding birds in 1970s), some 15 colonies each contains more than 1,000 birds. Farallons alone (world's largest colony) supported *c.* 28,000 nesting birds in 1979 and *av c.* 16,000 between 1971 and 1980 (del Hoyo *et al.* 1992; Johnsgard 1993) but has declined by 50% since 1970s (Nur and Sydeman 1999). Possibly 10,000–11,000 pairs along Pacific coast of Mexico. Population of this disturbance-sensitive cormorant greatly reduced by collection of eggs in 2nd half 19th Century and in some localities, including Farallons, by other human activity. Nur and Sydeman investigate the variables involved in assessing population trends (survival, probability of resighting, etc). Brandt's most southerly of 4 cormorants on Pacific coast of N America; overlaps with double-crested and pelagic, not with red-faced (most northerly).

MOVEMENTS: Largely sedentary; some dispersal S or (BC) N in autumn.

Foraging and food

Exclusively marine or brackish inshore waters. In exploiting upwellings of California current resembles guanay of Peru in relation to Humboldt and Cape cormorant of Benguela, though on smaller scale. Often travels in steady, flapping flight low over water, in lines or 'V's, between breeding colony or roost and feeding grounds. Apparently rarely feeds close to roost and may fly 25–30 km each way. Leaves early morning and returns midday–sunset. Fishes both in dense flocks on shoaling fish and individually. Johnsgard notes that switch from flock-foraging to individual fishing may occur rapidly and involve large numbers of birds. 46% total foraging alone, 54% with other cormorants or seabirds (Hebshi 1998) including guillemots, which may drive fish nearer to surface. Cormorants foraging alone fished over rocks more than sand, whereas in groups showed no preference. Both categories apparently avoided sites subject to heavy seas. When feeding on shoals, employs 'leap-frog' method found in several other cormorants. When feeding on bottom-dwellers in mud or sand dives deeply; often feeds over kelp. About equal numbers of schooling and non-schooling fish recorded in food samples (Johnsgard 1993, Table 25, for sp)



6.116 Distribution of Brandt's cormorant. (After Johnsgard 1993.)

which include (importantly) clupids, ammyndytids, engraulids, pleuronectids, gadids, scorpionids, gobiids. Takes crustacea; shrimps *Spirontocaris* and crabs *Oedignathus*.

Habitat and breeding biology

(See Fig. at end of ch. 5; Williams (1942) first to describe displays and provides one of best cormorant ethograms in literature, written when field ethology in its infancy.)

HABITAT: Likes small, rocky islands or coastal slopes. Nests on bare ground, often bouldery, inclining gently towards prevailing (breeding season) wind, but will use wide cliff-ledges and steep rocky slopes.

COLONIES: (Johnsgard 1993) 1–50 (41), 51–100 (17), 101–200 (24), 201–500 (30), 501–1,000 (11), 1,001–2,000 (9), 2,001–5,000 (3), over 10,000 (1). Nest-sites not limiting now but may well have been in past.

Main colony may have small outlying groups nearby, location of colonies may change from year to year, as does size and proportion of non-breeders within it—latter related to current availability of food. In large colonies nests may be densely and quite evenly dispersed, if topography allows, though always with gaps. On Farallons evidently some competition for nesting space with common guillemots; able to exclude cormorants by virtue of earlier occupancy and dense nesting.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually, but may miss very unfavourable years (see Nur and Sydeman 1999). Onset highly variable according to region and year (weather; dislike very strong winds). On Farallons begin to occupy nesting area early March–mid-April, occasionally not until May; first eggs laid 12 April–22 May. S California eggs (though rarely) laid as early as Dec but British Columbia late June–July. Intense sexual activity may last over 5 months. Old-established males return first. On Farallons seasonal decline in attendance retarded if local food remains abundant. Conversely, in warm years when food generally poor, all birds leave colony early.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Overt fighting with pushing, pulling and thrashing wings, tumbling over rocks; duration up to 3 min. Territorial threat on display-site chosen by male, thrusts head towards opponent with closed bill and distended gular pouch, ruffles plumes and partly lifts wings accompanied at extremity of forward movement by rapid twisting of head in short arc to right and left and hoarse, trilling growl. Old-established males occupy and roost at their sites early in season but unguarded in middle of day. Nesting group may accrue as consequence of single male settling on a site and advertising. If he acquires a female, other males may settle nearby, and advertise.

Ubiquitous cormorant advertising slightly modified; wing-flicking is rhythmical 'flutter', primaries oscillating rapidly, rather than series of discrete flicks, suggesting from rear a 'feather duster in motion'. Williams (1942) and Williams (1978) both remark on the paucity of vocalizations in this cormorant. May continue 25 sec. Bird squats, breast lowered, nape almost resting on back, bill pointing upwards; tail cocked and spread. Apparently head not rotated, though frequently may be twisted to one side. Seems to lack well-developed throwback and gargle. Head, neck feathers ruffled. During wing-flutter gular pouch bulges—'kink-throat'—exhibiting cerulean blue. After variable period head thrust forwards and down, bill gapes slightly. Thrust may be repeated up to 15 times before fluttering resumed. Females, with

necks thin and stretched, move between these swollen-necked, fluttering males, apparently selecting. May do so repeatedly over period of 2–3 hr, visiting many males. Often interact with 2 or more males, eventually settling with one. Approach or inspection by potential mate may stimulate advertising male to adopt head-down posture with head and neck horizontal, tail lowered, apparently similar to precopulation posture of female (indeed, reverse-mounting may follow such male posturing). At this stage female may jab male's head or neck, whilst male stretches and recoils. In this cormorant 'recognition' does not utilize 'throwback'; employs 'gaping'—forward movement of head with vocalization, resembling slow, highly stereotyped threat, much like 'pointing' used in other species.

Once established, pair may perform mutual billing, gripping each other's bill, and smooth necks over each other in typical cormorant fashion. Blue gular pouch focal point for each bird to nibble. If female remains on male's site for some time male fetches nest material, alighting long-necked, inflated gular pouch, head and neck feathers erected, back plumes raised. Female rises, grasps nest-material, both birds sway from side to side holding material before arching stiffly down with it. This behaviour, described (Williams 1942) as nest-material ceremony, is more highly ritualized version of depositing material than is found in most other cormorants, akin to its equivalent in flightless cormorant. May occur in male even if partner absent.

Pre-hop and post-landing (post-hop) postures distinctive, former involving highly arched neck with down-pointing bill, neck remaining arched during hop, latter an erect, forward-leaning posture with closed bill. Much used during movement around site. No specific mention of 'discoidal head'.

COPULATION: (GFA) Both birds may stretch upwards with extended gular areas displaying vivid blue pouch. In one pair, in 2 hours, Williams documents 4 copulations, 13 trips to sea by male for nest-material.

NEST: Variably sized mound of land-vegetation, seaweed, flotsam, guano up to 20 cm high but

rarely (ever?) sticks (usually no trees). Male gathers material but partners interact with it at site and both build it in. Pilfering common and established males rarely manage to accumulate material before acquiring a mate. Although nest-material picked up in colony, or on land, mainly gathered communally. Birds fly back and forth to vegetated areas or to patches of seaweed. Nesting gulls may have their nests filched from beneath them. Guano adds bulk.

EGG/CLUTCH: $61.05 \pm 2.96 \times 38.44 \pm 1.71$ $n = 20$, position in clutch unspecified. Weight: c51 g. Clutch 1–6, mainly 3–5 and 97% 2–4, most often 3. Farallons, mean 2.4–3.8 (1977–82). Clutch-size thus varies significantly with year. In some years more than half of all clutches contained 4 eggs. Overall 1.2% contained 1 egg; 16.6% 2 eggs; 57.1% 3 eggs; 22.7% 4 eggs and 2.4% 5 eggs $n = 483$ clutches. Within a given year clutch-size decreased through season except in certain years when, presumably due to upturn in food, it increased. In these aspects Brandt's typical of species affected by upwelling system in which they feed. Eggs laid at night or early in morning usually at 2-day intervals, sometimes 3-days. Av interval between egg 1 and egg 2 2.6 ± 1 , egg 2 and 3 2.5 ± 0.9 , 3 and 4 2.7 ± 0.9 , 4 and 5 2.7 ± 0.6 days.

REPLACEMENT LAYING: Occurs, except under adverse circumstances. Second clutches laid in 57% of 108 cases. In 6 cases 3rd clutches attempted and once 4th attempt made (Ainley and Boekelheide 1990).

INCUBATION: Shared; eggs never unattended under normal conditions. Incubation period: 170 eggs of first clutches av 29.9 ± 1.1 days. Because full incubation doesn't start immediately, position within clutch also had effect, 1st eggs taking c. 1 day longer than 2nd eggs; same difference between 2nd and 3rd.

CHICK/BROOD: Hatchling very dark. Closely brooded for first 10 days except in very warm weather. Brown body down grows rapidly, darker on back, though head remains naked until 5–6 weeks, by which time juvenile feathers developing. Between 10–20 days, growth rapid; activity such as

sitting up and preening increases. No special features of brood except crèching tendency.

CARE OF YOUNG: Closely brooded for first c. 10 days, except in very warm weather. Parents pass small morsels into mouth of small chick (Ainley and Boekelheide 1990); chicks insert head into parent's gape only after first few days. Once chicks left unguarded, first few days critical; immature or non-breeding cormorants may harass them, even on their nest, repeatedly pecking them. Small chicks thus displaced may die. Age left unguarded seems related to availability of food; in food-poor years, more young chicks unguarded. Again one sees this curious phenomenon of conspecific interference with no obvious advantage to interferers.

BEHAVIOUR OF YOUNG: Body-care increases noticeably 10–20 days. Chicks may leave nest before they can fly. Small chicks (10–25 days) from adjacent nests huddle together on a nest-site around time that adults terminate continuous attendance (Carter and Hobson 1988). Crèches occur mainly at night, probably conserve heat. Later, crèches occur at edges of nesting groups. Large chicks, more than c25 days, from several nesting groups, stand together sometimes right outside colony, nearer to sea. Fed away from nest.

FLEDGING: Seems gradual. No precise details. Fledging period 40–2 days.

POST-FLEDGING: Fed 'several weeks' (Ainley and Boekelheide 1990, who elsewhere say 20–40 days after they wander from nest). Period varies according to availability of food. Nest site often used as focus for post-fledging feeding though juveniles may have to chase adult to edge of colony before it regurgitates. Alternatively, free-flying young may be fed in a crèche.

BREEDING SUCCESS: Shows several adaptations which maximize reproductive success in an area of upwellings. Figures of Boekelheide and Ainley (1989) detailing 1971–83 particularly valuable as colony hardly disturbed, so avoid important source

of error. Hatched from laid: 0–89%; overall av 46% ($n = 1,555$, 51% one group, 41% another). Lower success in one group attributed to nesting among guillemots which led to more commotion and consequent egg predation by western gulls. In 2 years (1978 and 1983) all eggs abandoned in unfavourable feeding conditions (incursions of warm water) but this apart, little variation between years, nor, overall, between eggs laid early, middle or late in season. However, in some years such a difference did occur, but in all directions, early clutches faring best in some years but middle or late ones in others. Around 12% fully incubated eggs failed to hatch. Fledged from hatched: av 75%; Group 1 76% (0–93), Group 2 74% (60–92). Combining figures for all 13 years, no differences in fledging success between early, middle, and late nesters. Only in 1975 did early or mid-season nesters have obviously poorer success than later ones. Fledged from laid (given huge variation in hatching success, breeding success inevitably varies greatly between and within years): Group 1 39% (0–70), Group 2 31% (16–56). Fledged per pair: overall av 1.5 ± 0.9 ; Group 1 $0-2.6 \pm 0.6$, Group 2 $0.5 \pm 0.9-1.8 \pm 1.0$. Although number of chicks fledged increased with clutch-size, only difference between 2-egg clutches and larger ones significant, that is, 3-egg clutches produced as many fledglings as did clutches of 4 or 5, and 4-egg as many as 5. Number of chicks fledged per egg laid highest for 3-egg clutches, which is thus optimal clutch-size. During 2 warm-water years (1973 and 1976) many chicks died in their first month but in other years, such as 1975, only very young chicks died. Ainley and Boekelheide remark that Brandt's cormorant has highly variable breeding success. In more than half the years, most nests failed to rear even one chick. This trait apparently found elsewhere in its range, and, in some other cormorants, in extreme form in those species which rely on upwelling systems and are prone to abandon nesting if food becomes scarce. Typically birds produced 2–4 fledglings per lifetime. Both sexes av about same number of breeding attempts per lifetime; max 8 for males, 7 for females. Breeding success of males increased steadily with increasing age-experience but, per lifetime, females found to have produced more chicks than males (can happen because of changing partners). Nur and Sydeman

(1999) analyse success in relation to population dynamics on SE Farallon, especially population-size and food availability, concluding for success much depends on abundance of juvenile rockfish.

FIDELITY TO COLONY, SITE, AND MATE: As so often, depends on definitions. Usually remains within same general locality (say Farallon Island) having once bred there but may change nesting-group from year to year. Thus nest-site and pair-bond tend to be impermanent. Many pair-bonds last only one year (c90%) and virtually none lasts more than two. Even if male returns to site of previous year (c70% of 110 males did so) only 32% of 28 females who returned to group went back to last year's site.

Emigration of pre-breeders from general area of birth probably low.

AGE OF FIRST BREEDING: Despite both sexes returning to breeding colony at c. 2.7 years, females began to breed when younger than males, av 3.5 years (2–7) $n = 40$, males at 4.2 (2–9) $n = 70$. However, modal age of first-breeding by all known-age females 2.0 years, males 4.0. In great cormorant and European shag, by contrast, males breed when younger than females. Many young birds appear and attempt to breed in years when food supply good, but few or none in poor years (Boekelheide and Ainley).

NON-BREEDING YEARS: Occur as response to unfavourable conditions but not known otherwise.

LONGEVITY AND MORTALITY: Since males first bred at 4 (mostly) and av 8 breeding years, usual lifespan (taking account of years when did not breed) c. 14 or 15 years. Females apparently had slightly shorter lives. Implies that some Brandt's cormorants must live 20 or more years, high figure for a cormorant. Of 2,876 chicks ringed, 17% subsequently seen as adults at natal colony, implying, in absence of significant emigration (an assumption), a pre-breeding mortality of c80%, not unusual for a pelecaniform.

Adult survival significantly correlated with changes in abundance of juvenile rockfish and differed between sexes—77% male, 71% female (Nur and Sydeman 1999). Female but not male survival appeared age-specific; older females showed reduced survival especially in unfavourable (ENSO) periods.

European Shag *Phalacrocorax aristotelis*

PLATE 7

Pelecanus aristotelis Linnaeus, 1761, Sweden.

Sometimes assigned to *Leucocarbo* or *Strictocarbo*.

Other common names include: green shag or cormorant; common shag.

French: cormoran huppé. German: krahenscharbe.

Spanish: cormoran monudo.

Sub-species

P. a. aristotelis: Iceland and northern Scandinavia S to Iberian Peninsula, covering Faroes, Britain, NW France and Atlantic coast of Spain and Portugal. NW former USSR and northern Europe.

P. a. desmarestii: Mediterranean from France and Spain including most of islands, to Turkey and Black Sea. Vagrant, Red Sea. In northern Adriatic, of 122 islands, (1985–89) 19 occupied by breeding pairs.

P. a. riggenbachi: Rare. Atlantic coast NW Africa (Chafarinas Islands) but may be inseparable from *desmarestii*.

Description

ADULT M PRE-BREEDING: Black body plumage has strong metallic green gloss. Black edges to mantle feathers, scapulars, upper wing-coverts give scaly look. Tail black, glossed purple-green. Conspicuous recurved crest on forecrown. Bill blackish with yellow flanges, gape yellow, eyes emerald green with narrow yellow inner ring. Facial skin blackish. Legs, feet black.

ADULT F: Similar; crest smaller.

POST-NUPTIAL: Plumage noticeably duller, chin pale and mottled, crest disappears.

JUVENILE AND IMMATURE: Juvenile upperparts dark brown with faint greenish tinge difficult to detect. Dark brown edges to feathers of mantle, scapulars, upper wing-coverts broader than adult's, acquiring buff tips by abrasion. Chin whitish, throat pale brown. Sides of head, neck, most of breast, flanks dark brown; paler central underparts. Tail and

wing feathers black; underwing browner. By 2nd summer underparts still noticeably pale; darker feathers appearing elsewhere. 2nd–3rd autumn may acquire glossy adult plumage; traces of brown may persist longer.

Field characters

Overall green gloss and yellow gape and smaller size distinguish from cormorant even if crest absent. At distance and in poor light juveniles and immatures can be trickier since size deceptive, but shag slimmer, with slender bill. Browner below without extensive white and (often) lacking distinct pectoral band of juvenile cormorant. Faster wing beat.

Measurements (see Appendix)

An equation based on bill depth and wing length correctly assigns 94.8% to their appropriate sex (Calvo and Bolton 1997).

Voice

Male sonorous 'a-aarks' interspersed with throat-clicks, at breeding colony, typically with aggressive context—e.g. intrusion. Inflying males start calling 100–200 m from site. May call when leaving nest or when flying in to feed juveniles on sea-rocks. Female 'clicks' and hisses. Voices of male and female chicks become distinguishable at 5–6 weeks when females lose deep voice. Small chicks utter plaintive 'wee-ick'. Later, beg with repetitive 'wee-u' and threaten with hoarse 'wee-AA'.

Range and status

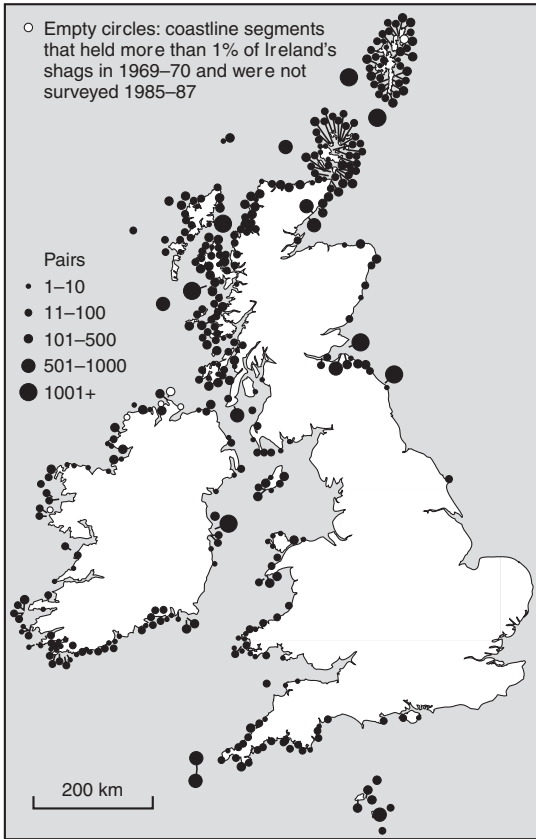
Nominate race far more numerous and widespread than *desmarestii*. Lloyd *et al.* (1991) suggest 70,000–180,000 pairs. Britain and Ireland accommodate more than 47,000 pairs. In Britain population tends to fluctuate far more than cormorants'. Between 1969–70 and 1985–87 numbers increased by some 25% and in Ireland by some 50%. Between 1905 and 1965 population in Farne Islands and Firth of Forth grew from 10 breeding pairs to c. 8,000 pairs at a rate of 11% per annum (Potts



6.117 Distribution of the European shag. Showing breeding range, main insular colonies and wintering range. (From Johnsgard 1993.)

1969). On Isle of May 1919–87 at 11% per annum, population reaching max *c.* 1,900 pairs. On Bass Rock 1961–97 fluctuated 10–300+ pairs (personal observation); 1997–2000 fewer than 30 pairs. Population in SE Scotland and NE England crashed in winter 1975–76, 1985–86, 1993–94. At present (1998) shags building up again but remain well below previously highest level. In Brittany small breeding population expanded at *c.* 5% per annum 1960–75 (Debout 1987); present French population 5,000–7,000 pairs. In SW Norway numbers fell by perhaps 50% during 1970s (Barrett and Vader 1984) though elsewhere in that country numbers maintained or even increased; population *c.* 15,000 pairs. In one area (Rogaland) population increased by some 20% per annum (Rov 1990,

who gives general information on Norwegian populations), an increase far above that which region's own productivity could generate. Breeds in Iceland—8,000–9,000 pairs. Faroes 1,000–2,000 pairs. Elsewhere in range, where populations smaller, trend during last *c.* 30 years has been downwards. Total Mediterranean population of *desmarestii* probably less than 5,000 pairs though some say 10,000, of which around 7,000 pairs on W Mediterranean islands, mainly Balearics, Sardinia and Corsica (Guyot 1993). Recent survey of numbers on Corsica (1978–94) by Guyot and Thibault (1996) revealed nests decreased in all areas except N, where new colony established. Decrease 55% overall (52–80% according to area) though number of colonies did not decrease. Actual nest totals



6.118 Distribution and size of European shag colonies (and grouped colonies) in Britain and Ireland, 1985–87. Note: the size of colonies can fluctuate greatly although their general location remains. (From Lloyd, Tasker and Partridge 1991.)

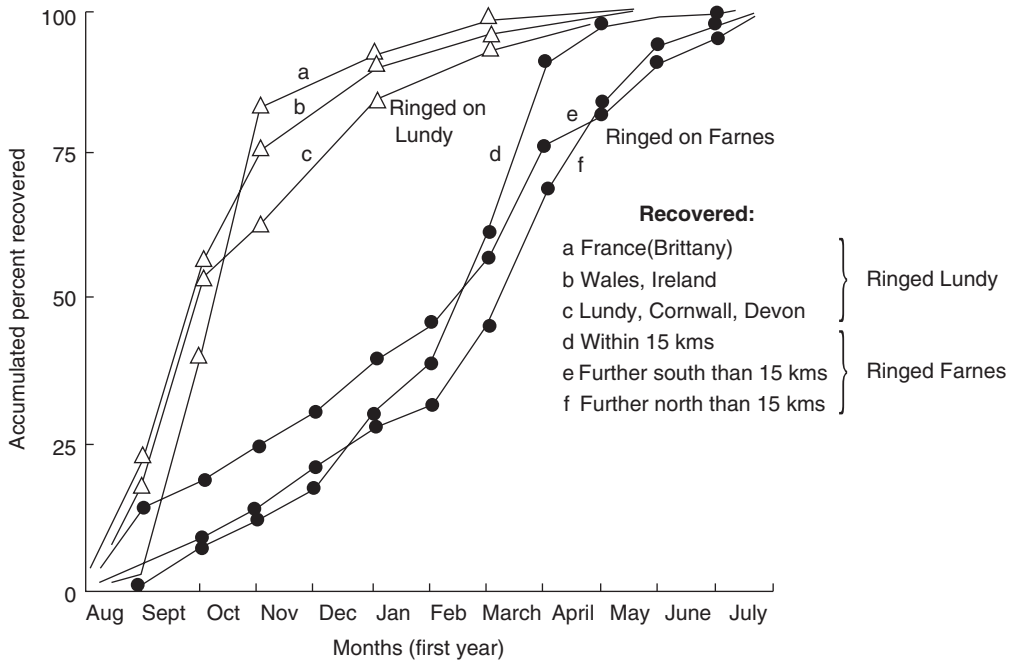
dropped from *c.* 1,000 (1982) to 320–75 (1994) thought to be caused by changes in food (not due to persecution, disturbance, or pollution). In Galicia (Spain) coastal colonies numerous and widely distributed but small (see Silvar and Rabago 1976). In Adriatic, breeding on 19 of 122 islands; total breeding population *c.* 500–688 pairs (Benussi 1990).

Whilst shag's tendency to withhold breeding in some years (Aebischer and Wanless 1992), presumably because feeding poor, together with variable timing of breeding, perhaps for same reason, do complicate census work, tendency for numbers to fluctuate quite considerably remains a real phenomenon.

MOVEMENTS: (Pioneer analysis of eruptions and dispersal by Potts 1969) By end 1995, 167,510 shags, mainly young, had been ringed in Britain alone, more than any other pelecaniform (great cormorant 59,015; gannet 59,969). Resident or coastally dispersive and eruptive on occasion, with occasional 'wrecks' after prolonged onshore winds. Extreme N populations may move S, though Icelandic birds seem resident. Extreme S populations (Med and Black Sea) mainly resident. Regional, annual, age-related differences in timing and extent of movement may occur (Galbraith *et al.* 1986). Many populations move less than *c.* 70 km; wintering areas of different populations appear to be reasonably discrete.

Foraging and food

Feed singly or, where several congregate, independently. Flocks of several hundreds may follow dense shoals of fish. Breeding shags usually feed within 10 km of colony. Mean foraging range Isle of May 7 km, max 17 km (Wanless *et al.* 1991) as Pearson (1968) had calculated for Farne Island birds. Wanless *et al.* (1998b) demonstrated that Isle of May shags made long-range trips (*c.* 10 km) and short-range trips (*c.* 0.8 km). The former were characterized by high diving efficiency (proportion of dive spent foraging) and low feeding rate (amount of prey caught/sec foraging). Short-range trips showed lower diving efficiency and higher feeding rates. Typically fly direct to feeding area, dive several times, remain on water 5–15 min and return to nest. During one foraging trip may feed in areas several km apart. Wanless *et al.* showed that Isle of May shags never went S or E and feeding areas, in effect 'patches', close to island or inshore, near mainland. Within the roughly 8% of potential foraging area used, shags fed mainly in water 21–40 m deep, over mixed sand and gravel or rock, generally avoiding deeper water over mud. Their preferences appeared, unsurprisingly, to match those of sand-eels upon which they fed. However, have been recorded diving 61 m, though foraging depth varies considerably between years and colonies (Wanless *et al.* 1997a). 47.6% underwater time spent foraging. Shags often spring clear of water before diving and may (rarely) plunge from air. Dives *av.* *c.* 40 sec but up to 3 min commonly reaching



6.119 Dispersal patterns of the European shag from two localities (South and North England). (After Potts 1969.)

33–5 m, sometimes deeper. A little more than half time submerged was at 25–34 m, close to seabed. Prey often caught mid-water but also taken from bottom. Av underwater swimming speed 1.7–1.9 m per sec (Wanless *et al.* 1997a). Mean dive 62.0 ± 1.92 sec; recovery time 84.4 ± 5.02 sec—much longer than in previous studies (Wanless *et al.* 1993b, using radio-telemetry). These authors suggest that, on longer dives, birds use an anaerobic mechanism. Bottom phase of dive can be varied according to availability of high-quality prey.

During incubation Isle of May birds made 1.4 feeding trips per day lasting av 4.75 ± 2.25 hours. Birds absent from nest >6 hours per day (Wanless and Harris 1992). When feeding young, number of trips doubled but each trip lasted less than half as long. Individuals varied substantially, but sexes did not. Some 32% of trip-time of incubating birds was spent actually diving but when feeding young this increased to 49%. Whilst away foraging, birds with young spent hardly any time ashore whereas incubating birds spent 42% of trip time ashore.

Foraging success age-related; during 1st year survival increases by 4.6% for every month bad weather delayed during their first autumn/winter. Mortality 1st-year greater on W and S coasts of Britain; stress may arrive sooner there (Potts 1969).

For list food species see Rae (1969), Cramp and Simmons (1977), Johnsgard (1993) (will exploit trawler discards, Oro and Ruiz 1997). Diet varies; sand-eels, clupeids, gadids predominate with shore fish, especially viviparous blennies, and crustaceans supplementing, or in case of shore fish, forming up to half diet in some areas. 87% of prey off Chausey Islands, France, sand-eels (Gremillet *et al.* 1998a; Wanless *et al.* 1998a for sand-eel consumption in N Sea). This prey taken even in winter and may be a major determinant of timing of breeding. Food loads brought back to Isle of May consisted almost entirely of lesser sand-eels *Ammodytes marinus* ranging from 8–208 g mean 106 (Wanless *et al.* 1993a). Daily intake c250 g (13.5% body weight); fish up to 20 cm taken. When feeding further from colony and when biomass of brood larger, adults

returned with heavier loads; daily fresh weight of food taken, including that brought to chicks, was 478 g (males) and 583 g (females) (Gremillet *et al.* 1996). Estimated to need 208 g per day for basal metabolism and can survive up to 12 days on reserves.

Use of pellets as analytical tool has limits; regurgitations during night often quickly disappear, either drying and fragmenting or eaten by gulls. Otoliths can be used to identify fish species. Barrett *et al.* (1990) report that, judged from pellets, diet of shag and cormorant overlap considerably, both relying heavily on small gadoids and sand-eels. Suggest predation by shags and cormorants could be one factor limiting recruitment of cod and saithe into now severely reduced stocks. Shags insignificant threat to fish farms (e.g. Carss 1993b). Nevertheless, possibly 700–2,600 killed each year (1984–87) at Scottish fish farms (Carss 1994).

Habitat and breeding biology

(See Fig. at end of ch. 5)

HABITAT: Essentially inshore marine though in some areas immature birds occur inland in winter. Prefers rocky coasts or islands with adjacent deep, clear water. Rarely strays as far as edge of Continental Shelf. Usually avoids shallow, muddy estuaries. Tolerates warm and cold water but not ice. At home in rough seas. On Aberdeenshire cliffs breeding low down on broad ledges, flat or sloping to at least 33°, with ample adjacent space. Evaluation showed that unused sites were entirely suitable (Olsthorn and Nelson 1990), so breeding population not always (perhaps rarely) site-limited. But on Lundy Island some bred on narrow ledges up to 60 m above sea level and with perpendicular rock faces above and below (Snow 1960). Will use gloomy crevices and caverns and often nest beneath overhangs or among boulders. Where local population appears to have occupied most of suitable areas (rare) may be competition for most protected sites and emigration, as, at one stage, from Farne Islands. Even where sites plentiful population may fluctuate wildly, as on Isle of May where varied from 364–1,129 apparently occupied nests between 1973 and 1980. On Canna

(Scotland) 1,690 nests in 1985 but only 436 following year, though more than 1,000 adults gathered on sea-rocks.

COLONIES: Usually of only moderate size though Isle of May (Scotland) has held c. 1,900 pairs and Runde (Norway) held 7,000 pairs in 1975, though down to 2,700 in 1981 (Rov 1990). Will breed solitarily. Colony density highly variable and depends much on topography of breeding locality. On flattish rocks or slopes nests may touch, but usually metres apart and irregular.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually (but 1993 c50% adults failed to breed, Isle of May, Scotland). Successful double-brooding recorded (Wanless and Harris 1997). Timing varies with latitude. In Britain experienced males may occupy breeding area in Feb–March and lay in March though usually April–June. Dates vary a great deal with year and laying date much affected by food. During 2 ‘crashes’ of Isle of May population (1974–76 and 1985–86) first egg almost month later than usual date (Aebischer 1986). Even in North Africa eggs seldom or never before Feb. In some areas breeding seems timed to coincide with availability of lesser sand-eels, abundant in inshore waters late March–April after winter spawning. On Farne Islands mean date first egg 12



6.120 Colony size varies between a few and several hundreds; rarely more than a thousand.

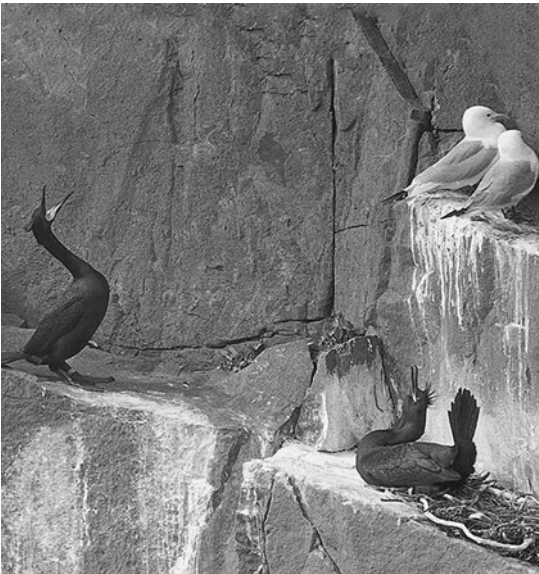
April (1972–86) whilst 85 km to N on May Isle 21 April (1962–86). Here date of first egg varied 23 March–20 May; very considerable spread. Length of breeding cycle including pre-laying attendance and post-fledging feeding some 16–20+ weeks; shags may be caring for offspring as late as October.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: (Figure 6.121; GFA; excellent account in Snow 1963, who details contexts of displays. Following fuller than for most species and provides useful bench-mark) Male establishes site. Overt fighting rare. In aggressive ‘threat-gape’ bird erects head and neck feathers, retracts head and shoots it forward with wide gape, displaying yellow interior. At full stretch head quivered from side to side with explosive ‘aark’ call. Low-intensity threat conveyed by staring and bill-pointing with distended gular pouch and slight lateral head-shakes. Apparent appeasement, ‘facing away’ and presenting nape, performed by parent to fledged young but seldom to another adult.

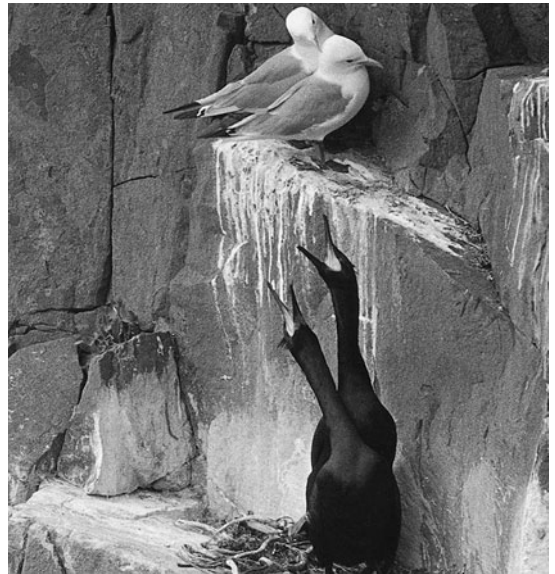
Male’s sexual advertising display consists of ‘dart-gape’ and familiarly ubiquitous ‘throwback’.

With body nearly horizontal male draws head back before rhythmically darting it up and forwards about once a sec, opening bill and displaying yellow gape. Fanned tail cocked and head feathers raised. As female approaches, throws his neck along his back, points closed bill upwards and quivers gular pouch. In this position bill continues slight upward jerks, rhythmically continuous with preceding dart-gapes. Throw-back held 3–6 sec.

Performs number of ancillary displays—ritualized behaviours closely tied to particular situations. ‘Landing gape’ follows hop or landing from flight. Looks down, gapes widely and holds head and neck back with sleek and upright body. Bill closes slowly and posture relaxes. Mainly performed when bird approaches or leaves nest. Departing bird may make 3–4 hops, each followed by landing gape. Association with movement and nest facilitates its use by male to ‘invite’ female to follow him to potential site after she has responded to his sexual advertising at a distant point. Is non-aggressive, as, also, is a behaviour which replaces it or is interspersed with movement, namely ‘upright run’, in which with elongated body inclined forwards,



6.121 Male European shag (right) ‘advertising’ to female, who is performing the ritualised gape. (Photo: N. Tinbergen.)



6.122 European shag, mutual upright gape (the opposite orientation to the forward threat gape). (Photo: N. Tinbergen.)

feathers flattened and bill pointing down, shag runs rapidly with short steps. Female may use it when leaving male's side during courtship and male when approaching nest-site. During on-site greetings mates lean over each other's necks and throat-click. Hyoid and thus yellow gular skin is lowered and pulsates with the clicks. Female throat-clicks when visiting male and he throat-clicks before and after copulation. Parents do it when returning to their brood. 'Sitting gape' is ritualized display associated with being in centre of nest and incorporating quivering or shaking of head. Normally directed upwards and sometimes bird holds piece of nest-material, emphasizing congruence of quivering with act of inserting nest-material. Sitting gape usually mixed either with nest-quivering directed to rim of nest, or with 'bows' (see below). Characterizes nest-relief; incomer does it upon gaining centre of nest, and outgoing bird stops doing it upon leaving nest. Also apparent response of sitting bird to variety of actions of partner. Female gapes in response to pre-mounting throat-clicking of male; soliciting female repeatedly gapes and bows. One of those movements which occurs in ongoing behavioural dialogues; precise motivation and function hard to determine. Basically cooperative and partly sexually motivated. 'Bow' usually, and when at nest always, performed from sitting position. Often follows throw-back or sitting-gape and away from nest-site performed almost exclusively by male. Snow considers it basically appeasing, encouraging female to approach male.

COPULATION: (GFA)

NEST: Often large and untidy comprising base of sticks, stems, stipes and flotsam and cup of softer vegetation such as grass, sea-scurvy, thrift, etc. Av base diameter 45–55 cm. Base may compensate for slope of site. Snow (1960) showed that pairs with large nests produced most young but she could not control for age and experience. Olsthoorn and Nelson (1990) found nests on damp sites particularly unproductive, probably small chicks chilled. Both sexes build, material brought mainly by male. Begins month (sometimes much longer) before lay-

ing. Material added during incubation and chick-stage. Pilfering common. Adults defaecate near nest, contaminating immediate area. By 14 days chicks, too, defaecate over rim. Prior to that, adults toss away contaminated material.

EGG/CLUTCH: 61.9 (56.5–68.7) × 38 (33.6–41.8) n = 315 (old sites, probably experienced females); 61 (57.5–67.4) × 37.7 (35.5–40.2) n = 33 (new sites and probably inexperienced). Egg weights for these two categories: 49.4 g (37.3–62.6) n = 272; 48.1 (41.3–56.8) n = 31. Egg weights and dimensions vary according to position within laying sequence. Coulson *et al.* (1969) examined this variation knowing, also, age of female. In 3-egg clutches (87% of all clutches in Norway) 1st egg usually smallest, 2nd largest, 3rd intermediate except when laid by very old females (8+ years) when largest. In clutches of 4 the 2nd and 3rd typically largest though both smaller than 2nd egg of a clutch of 3. As female ages she lays progressively larger eggs. Difference in mean volume of eggs laid by 2 year-old and 8+ year-old females 13%. In fact change in egg breadth and volume can be used to determine age-composition of birds in different groups or populations. Seasonal decline in volume per egg (10–11%) notably great compared say with kittiwake (4.5%), but kittiwake clutch-size declines much more than shag's. In both, energy used in producing clutches declines but method differs. In neither case does seasonal decline in availability of food appear to be responsible. Coulson *et al.* (1969) suggest that late-laying shags lay smaller eggs because insufficient time between beginning to nest and laying eggs for full development of reproductive system. Grau (1996) showed that egg-production imposes but a small feeding cost on female. Max daily food requirements during egg formation only 1.15 g per day additional protein and 34 kJ per day energy, to produce a clutch of 3. Moreover, egg formation slow (13.5 ± 1.2 days for yolk formation). Eggs laid *c.* 3 days after yolk formation complete. Clutch 1–6 eggs; on Lundy 447 clutches averaged 3.07 (76% 3-eggs). Elsewhere, also, 3 is commonest clutch. On Menorca *P. a. demarestii* clutches: 1 egg (6.3%), 2 (9.5%), 3 (79.4%) and 4 (4.8%). Eggs laid mainly at night or early morning, usually at 3-day intervals (sometimes 4 or 5).

REPLACEMENT LAYING: Common if clutch lost in first half incubation. Occasional after loss of small chicks. Pair may change nest site between clutches. Mean interval egg 1, clutch 1 (clutch incomplete when lost) and egg 1, clutch 2, 17.3 days (8–29).

INCUBATION: Starts with egg 2 though egg 1 covered; on top of webs which are inserted beneath eggs with shuffling movement, ventral feathers raised. Eggs easily kicked out if adult leaves suddenly. After hatching, adult may remove shells from nest. Adults spent 17.7 hours a day in colony (Wanless and Harris 1992) showing that even when not incubating each bird spent time at or near nest. Incubation period, 1st egg 36.1 days, 2nd 33.3, 3rd 31.2. Thus hatch more synchronously than laid (see Brood). Partners change over about twice a day.

CHICK/BROOD: Eggs chip at least 24 hours before emergence of hatchling (c34 g). Chick's dark skin soon becomes covered with dense, dark brown down though much of face remains bare. Egg-tooth disappears c. 14 days. By day 12 maintain stable body temperature and cease to vocalize during exposure to cold. By week 6 chick fully feathered with dark brown upperparts and flanks. Weight reaches asymptote c. 6 weeks and c. 1,700 g after peaking above that figure, young shags reaching slightly above mean female weight but below male's. Broods 2–4, usually fledge 2, commonly 3 occasionally 4. Within same brood, hatchlings from larger eggs significantly heavier than from small eggs and chick retains this advantage during development (Stokland and Amundsen 1988; Amundsen and Stokland 1990). Moreover, large eggs given to females whose own were small produced young heavier at all ages than those hatched from small eggs. Detailed analysis of various combinations of egg-size and foster-parentage showed that both egg-size and parental quality had an effect. 1st and 2nd eggs hatched only 11.7 hours apart but 2nd and 3rd eggs hatched 48.3 hours apart, thus putting 3rd chick at considerable disadvantage. By time chick 3 hatched, chick 1 already almost twice as heavy as it. Hatching asynchrony accounted for 95% of difference in weight of chicks and egg-size only 5%.

Weight begins to reveal sex during or after week 5 and even if numbers 3 and 4 in brood, males can outstrip females which came from eggs 1 or 2. But factors other than sex influence growth of individuals in brood. Snow (1960) found that 6 male chicks which happened to be number 4 in brood av, at various ages, 15.9% (8–27%) below mean for that age. For 3 females figures were 17% (9–23%). Chicks which hatch early in year may fall below av weight for their age. At day 7 or younger, 19 chicks hatched before 7 May (1957) av 17% less than chicks of same age which hatched later. Siblings do not show overt aggression in competition for food. Exchange experiments by Snow indicated that after about a month, by which time chicks could stray onto adjacent nests, strangers elicit hostile behaviour from adults.

CARE OF YOUNG: Sexes share brooding and guarding. Up to c. 16 days, brooding bird shuffles webs beneath chicks. In fine weather half stands. Attends young up to 3 weeks and then (but unusually) may leave them alone for up to c. 15% of day. Intentional shading of chicks claimed. Attendance stints 1–5 hours, mostly 1.5–2. Both parents feed chicks from day 1. Within 30 min hatching chick can move head and utter begging call and feeding recorded within this time. Considerable difficulty may attend food-transfer initially and very small chick fed more frequently by female than male. Fed 3 or 4 times each day, each feed involving 1–5 insertions of chick's head, fewest from oldest chicks. Adult swallows or tosses away spilt food. Once young have left nest adults preface feeding by presenting back of head in apparent appeasement, function unclear.

BEHAVIOUR OF YOUNG: Initial food-begging weak and uncoordinated. Can stand during third week and beg by reaching up to adult's gular pouch. Wing-beating during begging apparently not seen at nest, except by young birds ready to fledge (50+ days), possibly anti-falling adaptation.

FLEDGING: If topography allows, often stand off nest before fledging. Fledging period c53 days (48–58) but 55 ± 1 where no wandering possible.

POST-FLEDGING: After free-flying gather, sometimes in scores, on sea-rocks; fed there for as long as 100+ days (Snow 1960): 66–75 days (6 cases), 76–85 (14), 86–95 (13) and 96–100+ (6). Others indicate *c.* 3 weeks but birds not followed as accurately; may be regional variation. Snow observed perfectly healthy brood which fledged normally but subsequently neglected, died. Post-fledging support thus vital.

BREEDING SUCCESS: Hatched from laid: 71% (69–73, $n=893$, 4 seasons, Lundy). New sites much lower, 58% ($n=114$). Fledged from hatched: 87% (67–95). Fledged from laid: 57.4%. Fledged per pair: 1.87 (1.32–2.25) but marked discrepancies between years, between pairs nesting early versus late, and between experienced and inexperienced pairs. Only 0.9 young per pair fledged from probable first-time breeders against 2.3 from experienced. In all years pairs which laid by 3rd week in April fledged more young (2.8 per pair) than pairs which laid later, though advantage varied with year. By experimental manipulation Daunt *et al.* (1999) disentangled age effect from other possible influences and showed that old pairs consistently outperformed young ones. On Isle of May normal productivity 1.2 ± 0.04 chicks but in two crash periods (food shortage) it fell by 28% to 0.86 ± 0.09 (Aebischer and Wanless 1992). In May 1982 a gale destroyed 49% of 761 nests on Isle of May but 90% of affected pairs laid 2nd clutch 18 days after loss. By end of season, number of chicks fledged per pair 31% lower on side of island affected by gale (Aebischer 1993). In NW Spain chick mortality correlated with number of wet and windy days (Velando *et al.* 1999). This weather apparently correlated with marked reduction in sand-eels. On Menorca *desmarestii* fledged: no young (14.3%), 1 (9.5), 2 (49.2), 3 (25.4), 4 (1.6) (Pablo and Catchot 1992). Main causes of egg-loss, infertility, especially 4th eggs, predation after adult had left nest unattended for reasons not connected with predator, such as inadequate incubation behaviour, hunger due to unusual food shortage. Mortality among young due to starvation, inadequate care of hatchlings, disease, and, presumably after disturbance, predation. 47% of all young lost occurred before

day 10, 18% days 11–30, 13% days 31–40, 5% days 41–50. At undisturbed mainland-cliff colony in Aberdeenshire, excluding replacement layings, 119 pairs had breeding success of 55%. Of 102 broods 24.2% lost one or more chicks, losses unrelated to brood-size, 54% of chicks lost disappeared for unknown reasons weeks 3–4, a much higher figure than Lundy's. Damp sites produced 0.42 chicks per pair versus 1.79 dry sites (Olsthoorn and Nelson 1990). Sex ratio of chicks 50:50 (Graves *et al.* 1993a).

FIDELITY TO COLONY, SITE, AND MATE: Breeding birds strongly tend to remain faithful to same locality (breeding philopatry) but pre-breeders may move to colony other than natal one, though in shags ringed in colonies of Firth of Forth S to Farnes only 5% of birds ringed as chicks ($n=863$) recorded breeding away from natal colony (Aebischer 1995), similar to 78% philopatry of Farne Island shags recorded by Potts (1969). Females showed greater tendency to settle away from natal colony. Even among returners more females than males moved more than 300 m from birthplace. Some colonies lost more young birds through emigration than others. Aebischer found that large and dense colonies did not apparently exert stronger pull on young birds reared there than did a small, sparser colony. He also concluded competition for sites not cause of some shags moving away from natal colony. Of birds ringed as adults only 1% subsequently changed breeding colony. Once birds had recruited to a given area within a breeding colony (Isle of May) they stayed there (99.3% males, 97.9% females). Similarly, once having bred on Farnes, only 3 out of 750 found elsewhere. Fidelity to precise nest-site within colony is weak. Following details from Aebischer *et al.* (1995): Isle of May (1981–83) 76% of 3,038 nest-sites used in one year were reoccupied next, but ownership changed on one-third of reoccupied sites. Only 56% of surviving males nested on same site in consecutive years and figure for females even lower. But site-changers generally (87%) stayed within 16 m of previous site. Only half of 306 marked pairs bred together in consecutive years and the further the male moved from previous site

the less likely to retain mate. Divorce rate only 17% for males that did not move but 75% for males that moved more than 8 m. It is site-plus-male that is important for female. Only 6% of females bred on former site if former mate absent but 83% did so if he returned to it. Yet only 48% of females joined old mate on his new site, presumably because more difficult to locate, even if he had moved only a few metres. Seems surprising.

Young shags far more likely than adults to breed on sites that had not formerly been occupied and more likely than adults to change sites subsequently. Presumably, as grew older better able to compete for higher-quality sites. Since, also, they tended to move further, less likely than adults to retain former mate. Birds that move site have slightly lower breeding success than those who do not. Low incidence of simultaneous bigamy where good sites limited. Males may have several females at different sites throughout season.

AGE OF FIRST BREEDING: Usually 2–3 (2–5). Males 2 or 3 (24.6% 2 years $n=166$; 23.8% 3 years $n=161$); females mainly 3 (Harris *et al.* 1994b). In Brandt's cormorant, by contrast, females breed when younger than males (Boekelheide and Ainley 1989). Some first-year birds may form temporary pairs. When conditions favourable, up to 90% males and 50% females bred in 2nd year (i.e. 1 year + a few months old).

NON-BREEDING YEARS: Even when colony increasing (steadily or rapidly) may be considerable decreases year-on-year in breeding population. Number of nests on Isle of May dropped by up to 50% between 1974–76 and 1985–86, and whilst mortality may sometimes account for such decreases Aebischer and Wanless (1992) concluded that adult non-breeding is adaptation to environmental conditions, probably food. Emigration, high adult mortality and low recruitment considered inadequate explanation. Indeed observation showed that large part of population on Isle of May may abstain from breeding; nests increase to peak in early June but significant number never receive eggs. Some

sites occupied by more than one pair but none breed there. In 1993 about half Isle of May shags failed to breed (Harris *et al.* 1998). 66% of non-breeding birds were aged 14–21 but only 12% aged 3–6 years. In Feb 1994 bad weather caused very high mortality and individuals which survived best were aged 7–16. Among this age group, those which had not bred the previous summer survived better than those which had. Yet this apparent effect of breeding on winter survival was not apparent among youngest and oldest birds, which seems odd. Similar decreases in breeding population, but in presence of very large numbers of non-breeding adults, has been recorded on Canna, off W Scotland.

LONGEVITY AND MORTALITY: Annual adult mortality variously given as: male 15%, female 20% (Potts 1969); av 13% (Aebischer 1995); av 14% (Coulson and White 1957 based on live recaptures); 14.6% (Aebischer and Wanless 1992) and 12% (Snow 1960). Last figure based on failure to return to previous site and therefore likely to err on high side; based on survival of colour-ringed birds only 7%, which may be representative of adults during their prime years. Harris *et al.* (1994a), based on large numbers of retraps, give adult mortality as 12.2% (1963–87). Catchpole *et al.* (1998) using recovery and recapture data, calculate annual mortality 13% for birds of breeding age; 30% for birds in 2nd and 3rd years. Harris *et al.* found survival declined in birds older than 13 years. Male mortality may be lower than female, though evidence inconclusive. Almost all deaths occur during autumn, winter, and early spring, and rate varies greatly from year to year. Whereas Lundy birds died mostly in autumn those from Farne Islands tended to die in winter and spring. Mortality of first-year birds for 10 different areas averaged 61%, median age of death during this first year being 135 days. On Isle of May mean first-year mortality rate (excluding birds which fledged during periods of population crash) was 46%. For birds fledging during crash periods it was 62.3%. Mortality rose higher than 65% in 7 out of 24 cohorts for which it was determined. Two of the high mortality rates (1965 and 1983 cohorts)

corresponded to massive eruptions of shags from E coast of Britain in late winter and many found dead or exhausted along S coasts of North Sea in early 1966 and 1984 (Aebischer and Wanless 1992). In late breeding years winter mortality starts exceptionally early, presumably because young have not been fledged long enough to learn to cope. After first year, mortality not closely related to age. Snow (1960) estimated that c86% of fledglings die before breeding age. Harris *et al.* (1994a) surveying the results of large scale ringing (1963–87) and subsequent recapture of Isle of May chicks, found that

survival between fledging and 3 years ranged from 2.5–12.6%. They treated the Isle of May as a closed colony. Estimated survival was highest in young which fledged early in the season and higher in chicks from broods of 3 than of 2 (12.3 and 10.8% respectively—huge samples). It was lowest in single-chick broods (7.1%). Recoveries suggest shags need several months before foraging skills are sufficiently well developed to overcome adverse weather conditions. Among adults, birds with poor breeding success suffer higher mortality outside breeding season.

Pelagic Cormorant *Phalacrocorax pelagicus*

PLATE 7

Phalacrocorax pelagicus Pallas, 1811, eastern Kamchatka and Aleutian Islands.

Placed by some in *Leucocarbo* after Siegel-Causey (1988).

Other common names: pelagic shag, Baird's cormorant, resplendent cormorant. French: cormoran pélagique. German: meerschabe, nordpazifischen-kormoran. Spanish: cormoran pelagico, pato sargento.

Sub-species

P. p. pelagicus, breeds to species' northern limits: N Pacific (Alaska, Bering Sea, Arctic Ocean and coastal North America).

P. p. resplendens, coast of British Columbia south to NW Mexico. Population in between, from Queen Charlotte Island to Vancouver Island, not yet assigned. Birds of Siberian mainland and Wrangel Island are larger than Bering Sea birds and have been given sub-specific rank *P. p. aeolus*.

Description

ADULT M PRE-BREEDING: A black shag enlivened by metallic green and purple gloss. Two recurved crests on head (anterior one conspicuous but posterior insubstantial), white filoplumes on rump, back and neck; conspicuous white flank patches. Gular

and facial skin (but not forehead) reddish, gape red, bill blackish, red at base, eye green. Legs, feet black.

ADULT F: Similar.

POST-NUPTIAL: Loses crests, white flank patches and dispersed filoplumes. Facial skin dulls to brownish orange.

JUVENILE AND IMMATURE: Upperparts dark brown or black; underparts paler and duller, head, neck greyish. Face skin dull pinkish, eyes brown. Legs, feet blackish. As matures becomes mixed brown-black with increasing gloss. Face reddens, gape becomes red. Moults into adult plumage begins year 1, completed year 2.

Field characters

Small to medium-sized. Nearest relative very similar red-faced cormorant which shares much of its range in N Pacific. Pelagic lacks red skin on forehead and the blue gular skin and yellow on bill and is smaller, with slenderer bill than red-faced, Brandt's, and double-crested. In nuptial plumage distinguished by white flank patch. In winter, adults lack buff band below pouch which characterizes Brandt's, and lacks orange pouch of double-crested. Juveniles difficult to distinguish from red-faced, except that pelagic has less facial skin, but have darker underparts and much more uniform than juvenile Brandt's or red-faced.

Measurements (see Appendix)**Voice**

Usual cormorant croak and more explosive 'bark'; also hisses. Females 'tick' and call 'igh-ugh'; males 'purr' (greeting calls).

Range and status

Exclusively marine; bird of cold inshore waters and inhospitable coastlines, 'foggy and windswept' in words of Ainley and Boekelheide (1990). Nevertheless most widely distributed of 6 cormorant species in N Pacific and Russian far east. Breeding range centres along vast sub-arctic rim of N Pacific from N Japan (Hokkaido and N Honshu), Kurils and E Siberia eastwards through Komandorskies, Aleutians and Gulf of Alaska, thence along Canadian coast, including Queen Charlotte and Vancouver Islands, and American coast including Coronado Islands and Farallons, S to cold waters of Californian current. Johnsgard (1993 and refs) assesses main breeding populations: Canadian Pacific *c.* 9,000 individuals in 85 colonies; Alaska 150,000 birds in 285+ colonies, of which *c.* 40,000 birds in Aleutians; USA 28,500 birds, making *c.* 130,000 adults in N American population.

Hobson (1997) details distribution in Americas. Further 50,000–60,000 in Kuriles, *c.* 1,700 along Siberian coast, hundreds on offshore islands. Estimate of world population hampered by incomplete knowledge of Asia.

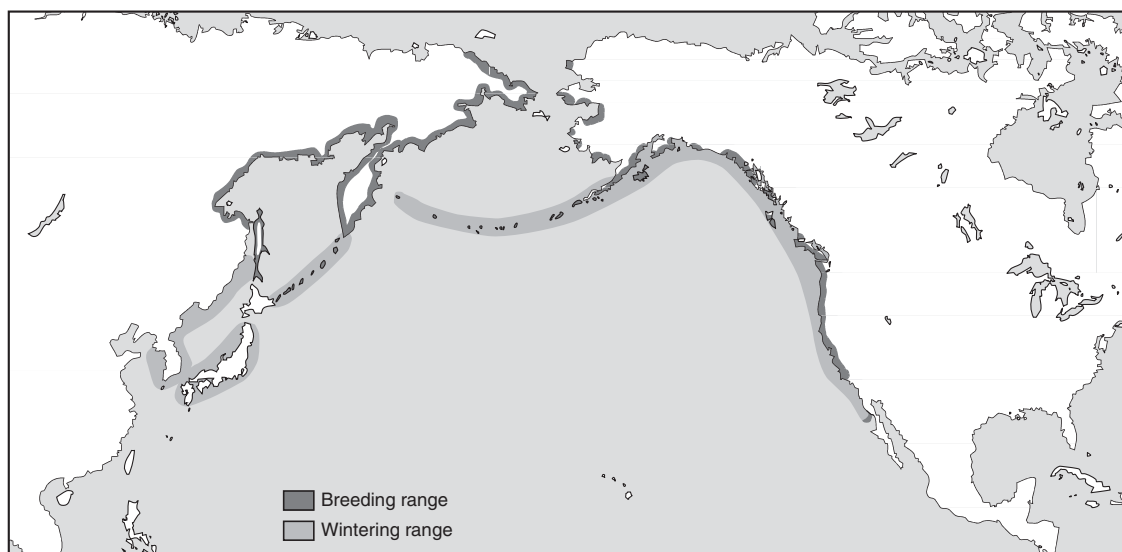
As widely dispersed cormorant with fairly small colonies often (usually 1–50 birds but very occasionally more than 500) on inaccessible cliffs, not as subject to massive disturbance as some ground-nesting species. Natural predation at breeding colonies, though locally significant, in no way threatens its secure status. In some localities increasing.

MOVEMENTS: Northern populations may move to escape ice. S of Queen Charlotte Island generally sedentary with a few wider dispersers (Hobson 1997). Movement up to 576 km recorded.

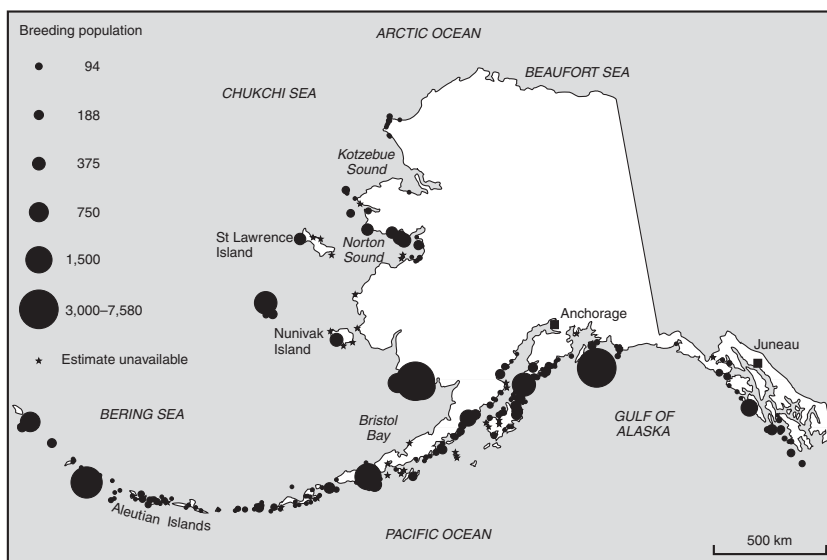
Foraging and food

(Details Hobson and Sealy 1985; Hobson 1997.)

Usually near coast in water up to 100 m but presumed pre- and non-breeders sometimes further offshore in much deeper water such as Gulf of Alaska and Bering Sea. Occasional inland on lakes



6.123 Breeding and wintering range of the pelagic cormorant. (After Johnsgard 1993.)



6.124 Pelagic cormorant colonies of Alaska. (From US Fish and Wildlife Service; Alaska Seabird Colony Catalogue.)

and rivers near coasts. Usually individual feeder, often solitary in turbulent inshore water mainly over reefs and rocky bottoms but also over sand or mud. Joins feeding gulls and other species and may attempt piracy. Of 53 mixed feeding assemblages 17% contained pelagics (av 4, range 1–10). Dives to 30 m or more (possibly >100 m), submerging for up to 70 sec. Immatures submerge about as long as adults and have longer mean dive times, probably because take longer to locate food. No difference in capture rates per complete foraging bout between adults (10.8% success rate) and immatures (11%). Prey largely non-schooling, bottom-dwelling fish, often cryptic, and crabs, but diet very general and varies with area. Farallons highly dependent on mid-water shoals or rock-fish (*Sebastes* spp) (Ainley *et al.* 1981). Little if any overlap with commercial fishing. Diet overlaps almost totally with Brandt's, considerably with red-faced, but less with larger double-crested cormorant.

Habitat and breeding biology

(See Fig. at end of ch. 5; Hobson 1997)

HABITAT: Marine cormorant of rocky coasts and offshore islands. Often nests below overhangs or in

cavities and will use sand spits, flotsam and artefacts such as beacons and bridges. Gregarious and often mixes with other cormorants, gulls, and auks. May breed in same locality as double-crested, Brandt's and red-faced although on islands where latter common pelagic tends to be rare or absent (Johnsgard 1993), perhaps partly due to exclusion from optimal breeding sites. Other ledge-nesters such as guillemots and kittiwakes may compete with pelagic, sharing its ability to use narrow ledges on precipices.

COLONIES: Large, dense colonies impracticable and pelagic often nests in small, linear groups or singly and, despite figures cited below, is considered the least gregarious of North American cormorants, typically nesting so that few are visible or close to others. Nevertheless a record cited in Palmer (1962) speaks of a great colony on St. Matthew Island, Alaska (1904). Av size Alaskan colonies fewer than 200 nests: 1–20 (96), 21–40 (29), 41–60 (24), 61–80 (7) 81–100 (6), 101–200 (7), 201–300 (6), 301–400 (3), 401–500 (1), 701–800 (1), 1,001–2,000 (1), 2,001–3,000 (1) (US Fish and Wildlife Service). Density depends partly on topography but typically 0.5–2+ m. Nests often vulnerable due to bird's

habit of flying far out to sea when disturbed. Like many cormorants, moves between nesting locations or even between islands in successive breeding attempts. Suspends breeding in highly unfavourable years—ENSO. Pre-breeders in large numbers evidently associate with breeders all year though less tied to colony and forage further afield.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually. On Farallons many individuals and pairs attend good sites throughout non-breeding season, which varies considerably in duration according to weather (Ainley and Boekelheide 1990). In some years many birds begin building Dec–Jan only *c.* 3 months after vacating colony (if they did). In other years birds inactive until May, depending principally on food. Usually last cormorant species to begin laying. First egg av 17 May (28 April–30 May) but span of clutch-initiation 2 weeks to 3 months. More than half all eggs laid within 2 weeks or less. Early years differed from late; in former, laying dates skewed and laying periods extended whilst in late years laying normally distributed. Further N than Farallons egg-laying later. At Mandarte Island extends from mid-May to early August, peaking mid-June, though late clutches are persistent replacements. On Vancouver Island most eggs laid early June to early July. In Gulf of Alaska primary egg-laying more closely restricted, 1st eggs occurring 23 May–3 June. Laying usually finished by end of June. Shorter and more predictable breeding seasons restrict egg-laying accordingly.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Overt fighting, grappling with locked bills, during competition for, and defence of, site. Correlates with relative scarcity of sites; fighting more frequent after most of persistent nests remaining from previous season had been taken and after density had increased (Siegel-Causey and Hunt 1981). Aggressive-defensive threat, darting head with wings ajar and bill gaping accompanied by growls.

Male selects site and ‘advertises’ to female. This species’ variant of male’s sexual advertising display

common to all cormorants consists of rapid, simultaneous wing-movements in ubiquitous head-up posture. Tail, in some species cocked, here held level or depressed. Wing-flicking given in irregular bursts of *c.* 2–6 sec. As in great cormorant, movement often ‘flashes’ white thigh. Head moves slowly from side to side but no full throwback and rotation or vocalization (Van Tets 1965). Displays usually interpreted as ‘recognition’, when both partners present, include gaping (colourful lining) with head moving vertically up and down in slow, stereotyped manner, bill open. Male utters prolonged ‘arr-arr’ and female repetitive ‘ugh-ugh’. Pelagic has conspicuous pre-hop posture. During ritualized hop, e.g. around nest-site, neck arched and gaping bill pointed down. Before take-off gaping bill turned towards direction of intended movement though feet may remain pointing inwards, so that neck twisted. After landing, neck lengthened with bill forwards and slightly upwards. Often ‘kink-throats’, e.g. when pair together and touching nest-material.

COPULATION: (GFA)

NEST: Male gathers most or all material; mainly seaweed, grass, and detritus but not usually sticks (these characteristic of double-crested cormorants nesting nearby). Incorporates man-made material but may build solely with coralline algae, seaweed, and guano. Pelagic excretes onto sides of nest, thus cementing it to sometimes precarious site. Nest may be substantial and persistent, but occasionally extremely flimsy (probably 1st-time breeders?). Size varies but *c.* 44 cm base diameter and 26 cm high may be typical.

EGG/CLUTCH: $58.85 \pm 3.83 \times 37.37 \pm 1.23$ (ignores position within clutch). Weight 44.6 g *n* = 143; 2.6–2.9% mean weight of female. Pre-DDT shell thickness (Alaska) 0.317–0.596 (details Hobson). No information on post-DDT thickness. Eggs laid 1 or more, usually 2, days apart (late-layers more than 2) and incubation, or at least attendance, begins with first egg. Clutch-size decreases as season progresses. Mean clutch-size (summarized Johnsgard 1993): Norton Sound 3.5; Cape Pierce 3.1; Gulf Alaska

2.17–3.52; Mandarte Island 3.8; Farallons 3.4 (1–5) and 90% of all clutches 3 or 4. Variation in clutch (different years, same locality) about equals variation between regions; *c.* 0.26–1.35 eggs. Unfavourable feeding may totally inhibit laying. In 1978 and 1983, Farallons, pelagic cormorants did not lay at all even though in 1978 more than 80% of sites occupied in readiness. Attributed to delay in seasonal upwelling in area. Similarly in Semidi Islands (Alaska) up to 80% site-owning pairs may fail to breed. Comparable instances occur in some other cormorants and more widely in *Pelecaniformes*.

REPLACEMENT LAYING: Persistent replacement sometimes characteristic of this cormorant and can account for much of variation in mean laying dates. However, on Farallons, birds losing first clutch generally did not re-lay, particularly in years when many pairs abandoned clutches or even broods, which this cormorant readily does in response to unfavourable conditions thus causing complete failure of breeding in entire colony. Of 80 pairs that lost clutches only 5 replaced them, producing 6 young (Ainley and Boekelheide 1990).

INCUBATION: Shared. Change-over 2–3 times per day. At Farallons (Ainley and Boekelheide 1990) 3.3–5.4 change-overs per daylight hours; time away from nests with eggs 123–248 min. Female incubates at night. Incubation period 31 (27–37 days); 29.5 (25–33) *n* = 110, Farallons, Boekelheide *et al.* (1990). 70% hatch 30–2 days.

CHICK/BROOD: Hatchling *c*27–40 g. Dark skin becomes covered with grey or sooty primary down below which develops a pale underdown. Gular skin pale or pinkish. Legs and webs blacken progressively. Head remains sparsely covered until true feathers develop. First plumage dark brown with hint of green gloss, paler on breast and belly, facial skin pinkish-grey. Hatching to day 5 grows slowly, then rapidly; max growth *c*60 g per day, days 5–8, maintained to day 25. By 3 weeks may weigh 1,150 g, full size attained 7–8 weeks. Brood presumably 2–3, occasionally 4, since av clutch size more than 3. No information on scale and nature of any brood reduction, but fledglings per successful

pair routinely 1 or more chicks fewer than clutch size for that year (Ainley and Boekelheide 1990: Table 6.3).

CARE OF YOUNG: Fully shared. No special features. Brood young for at least 3 weeks after hatching. Then leave them unguarded for *c*25% each daylight hour (Cannon 1990). Percent time shading young drops sharply after 3 weeks. Time away 91–191 min and 5–8.6 trips per day (Farallons). Egg shells not systematically removed, but tossed out eventually.

BEHAVIOUR OF YOUNG: After *c.* 1 week begin to defaecate over nest-rim and to stretch, yawn and preen. From 2 weeks exercise wings. Presumably young from narrow ledges on high cliffs remain on nest until able to fly competently, whereas young of many cormorants tend to wander. However, not a fixed response and where topography permits chicks may venture out of nest when 3–4 weeks old and join others in communal area where may be fed. Such chicks may return to nest. By week 7 said to be able to fly; begin to swim and bathe. These schedules must be modifiable according to nesting habitat. Unattended, pre-fledged young may be attacked by conspecific intruders; young crouch and bill-tuck.

FLEDGING: On Farallons most chicks fledged (*i.e.* departed nest) 45–50 days (30–59) *n* = 10, similar age to Mandarte chicks (42–58). Larger broods (4 or more) take several days longer to fledge.

POST-FLEDGING: Not recorded. Presumably young from precipitous sites return to nest or to top of cliff to be fed, if no sea-rocks.

BREEDING SUCCESS: Hatched from laid: up to 71% unless abandoned through food-shortage; 32–69% (3 locations, 6 years, Gulf of Alaska, Nysewander 1986); 47.9% (early laid 59%, middle 54%, late 22%, *n* = 891, 13 years, Farallons, Ainley and Boekelheide 1990). Most losses due to desertion; *c.* 12% eggs disappeared around hatching but maybe loss of hatchling rather than egg. At Mandarte Island predation accounted for 63% of 71 eggs lost in one year (Drent *et al.* 1964) but disturbance presumably

a factor here, whereas on Farallons specifically avoided. Predators include crows, gulls, and less commonly eagles and mammals (red fox, otter, mink). Fledged from hatched: 43–93% (Alaska); 61% (0–94%, early 64%, middle 59%, late 62%, 13 years, Farallons). Fledged from laid: 0.33–1.86 (Alaska, which compares with initial brood-sizes of 2.09–2.88). Thus in some years considerable mortality within broods, presumably due to sibling competition for food—even in most productive years some chicks starved; 29% (0–66%, Farallons). This range, including complete nesting failure or failure to lay in 4 out of 13 years and a further 4 years limiting breeding success to <20%, most extreme of any cormorant species breeding there. Breeding success correlated with proportion of juvenile rock-fish in diet for 3 years with data. Young rock-fish shoal in mid-water; presumably a staple food in this locality. Fledged per successful pair: 2.0 (Mandarte); 1.69–2.64 (1984–95, Anacapa Island, Hobson 1997). Strong relationship between mortality and slow growth of chicks. Heavy rain can kill many.

Unusually large oscillations in productivity in this cormorant, more akin to those which depend

on food-rich upwellings, correlate with its unusually rapid growth.

FIDELITY TO COLONY, SITE, AND MATE: May move between nesting groups on an island, or between islands. Has been suggested that disturbance or unfavourable natural factors such as predation or food, may precipitate move but highly likely that, as in other cormorants, such moves are also normal part of its breeding biology unrelated to specific events. Such behaviour incompatible with long-term fidelity to particular nest-site and mate, though in cases in which good site retained through non-breeding season, it (and perhaps pair-bond) may persist for 2 or 3 years.

AGE OF FIRST BREEDING: 2nd or 3rd year.

NON-BREEDING YEARS: Occur when food scarce. Non-breeders (which presumably include pre-breeders and possibly 'resting' birds occur in large numbers within and near breeding colonies.

LONGEVITY AND MORTALITY: Oldest known bird 17 years 10 months. No details of mortality rates.

Red-faced Cormorant *Phalacrocorax urile*

PLATE 7

Pelecanus urile Gmelin, 1789, Kamchatka.

Now sometimes placed in *Leucocarbo* or *Stictocarbo*.

Other common names: red-faced shag; violet shag. French: cormoran à face rouge. German: Aleutenkormoran, rotgesichtscharbe. Spanish: cormoran carirrojo.

Sub-species

Monotypic, but extremely closely related to pelagic cormorant and, apparently, museum identification of skins sometimes confused.

Description

ADULT M PRE-BREEDING: Another dark-all-over cormorant with sheens of green, blue, dark bronze-green or violet. No very distinctive patterning of feathers on back, wing-coverts or scapulars. Two median crests of green feathers one on crown and another on nape, conspicuous patch of white filoplumes on flanks and scattering of white, club-shaped filoplumes, 25–38 mm long on neck and rump, and in few cases on breast. Name aptly reflects bright orange-red area of engorged skin on forehead, lores and around eyes. Eyes light brown, bill pale blue towards base of upper mandible (tip and ridge dark) whilst lower mandible yellowish at base. Gape bright blue, also gular pouch, which is

bordered with corrugated yellow or purplish-red skin. Legs, feet blackish.

ADULT F: Similar.

POST-NUPTIAL: After (sometimes even before) eggs laid crests and white filoplumes and (later) flank patch, disappear; soft parts become duller, bill pales.

JUVENILE AND IMMATURE: Juvenile dark brown with paler underparts; slight purple gloss on upperparts. Eye light brown, bill dark horn, sometimes yellowish, tinged with blue at base, face flesh-coloured, eye-ring tinged green and legs and feet dark brown. Gives way to adult plumage by gradual development of colours and gloss.

Field characters

Under less than favourable conditions can be difficult to distinguish from pelagic cormorant with which, in places, it overlaps. Red-faced larger with stouter bill and bare forehead becomes distinctive once past juvenile stage. Adult, gular pouch blue

rather than red of pelagic. Red-faced only one in its range (N Pacific) with bare, red forehead. Juveniles and immatures must be recognized by size, bare forehead, face of brownish-red, or grey.

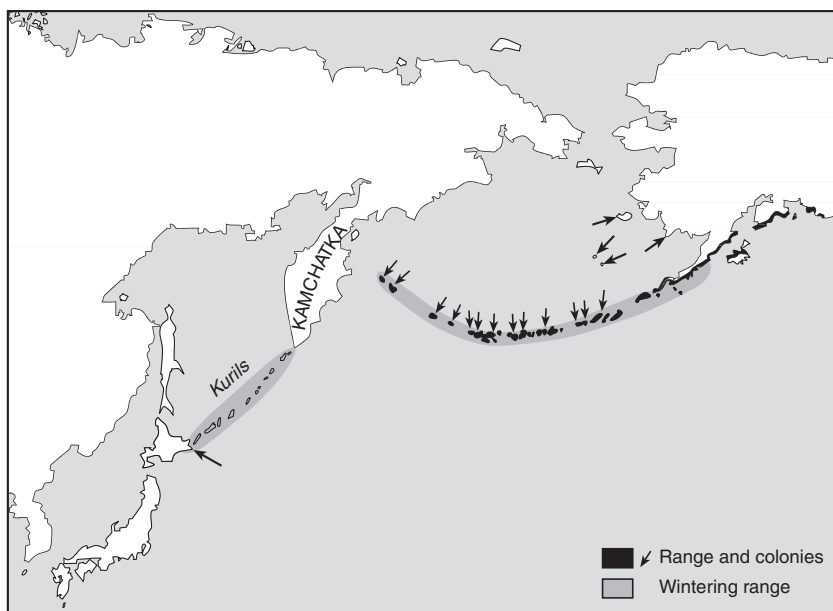
Measurements (see Appendix)

Voice

Little information beyond usual guttural croak. Males 'purr' in display; females 'tick'.

Range and status

Breeds in long, narrow arc from Gulf of Alaska and on islands W across Aleutians and more recently SW along Kuriles to Nemuro Peninsula (Japan). On Hokkaido coast *c.* 500 birds. Breeding range includes Commander, Pribilof, Nunivak, Aleutian, Shumagin and Kodiak Islands. On Kuriles *c.* 20,000–30,000 birds breed, (Johnsgard 1993) and some breed in S of Kamchatka. Golovkin (1984; in Johnsgard 1993) estimated at least 12,000 pairs in Bering Sea; others in Sea of Okhotsk and Sea of Japan. Apparently increasing



6.125 Distribution of the red-faced cormorant. (From Johnsgard 1993.)

in S Alaska and Aleutians where breeds fairly evenly from Unga and Amak Island and Port Moller through to Attu. Alaskan population \approx 150,000 birds whereas in 1970s thought to be \approx 130,000 birds, principally in Near Islands (88,000). Palmer (1962) suggested breeding stations may have quadrupled in past few decades.

MOVEMENTS: Generally remains in vicinity of breeding areas unless frozen out, but some move SW along coast and islands.

Foraging and food

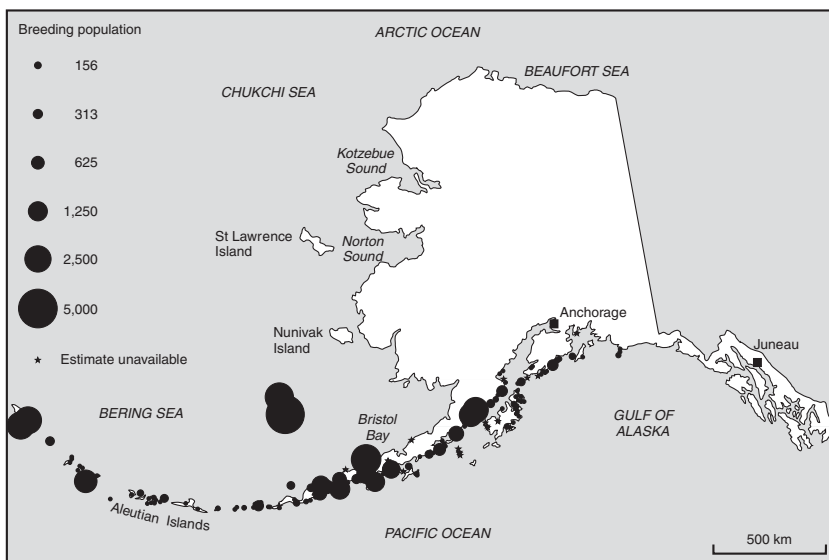
Rocky bottoms usually inshore (1–2 km), rarely as far as 5 km offshore, never in very deep (>100 m) water. Breeders usually forage within 3 km of colony. Searches out well-hidden bottom-prey such as cottids, shrimps, crabs (especially) and other invertebrates, although by far greatest part of food is fish, mainly cottids but also pollack and sand-eels. Red-faced and pelagic cormorants take much same food spectra although quantitative differences due to differences in body-size may well occur. For analysis of stomach contents see Hunt *et al.* (1981).

Habitat and breeding biology

(See Fig. at end of ch. 5)

HABITAT: Steep slopes and cliffs, often preferring lower sections and using both broad and narrow ledges though perhaps not as narrow as cliff-adapted pelagic cormorant (not measured, Nysewander 1986). In addition to possible competition with pelagic, it may lose in competition with fulmars, guillemots, and kittiwakes (Squibb and Hunt 1983).

COLONIES: Nests in small, loose groups, often linear, or scattered in twos and threes depending on availability of ledges. Alaskan colony sizes (nests): 1–20 (54), 21–40 (14), 41–60 (8) 61–80 (4), 81–100 (3), 101–200 (3), 201–300 (3), 301–400 (1), 401–500 (1), 501–600 (1), 601–700 (2), 701–800 (3), 901–1000 (2), 1,001–2,000 (5) (USFWS). Apparently may abandon breeding locality for no obvious reason and breeding population may fluctuate greatly from year to year. Number of active nests at Ugaiushak and Chowiet, Gulf of Alaska, increased fourfold from one year to next. May be substantial number of non-breeders in breeding colonies.



FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually; eggs early May to early June depending on region. On Pribilofs peaks mid-May; on one of Semidi Islands first layings varied widely between years but synchronized each year. Mean laying date 2 weeks either side 26 May; reflects strongly seasonal constraints and climatic fluctuations between years. Chicks fledge mid-Aug onwards.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Resembles pelagic. No details of territorial behaviour but may be well developed (competition for ledges).

Advertising males hold head backwards and upwards and move it up and down at same rate (twice per sec) as wing-tips raised and lowered, but not in synchrony. Movement alternately reveals and hides white thigh patches. Probably lacks full throwback and rotation of head. Partners meeting on site gape and move head up and down *c.* 2 times per sec, opening bill with each upward movement. During this recognition display male 'purrs', female 'ticks'. Also 'kink-throats', performs neck-arched pre-hop posture and a special pre-take-off posture in which, with gaping bill, bird twists its body in direction of departure. After landing, elongates neck and body and vocalizes (same in both sexes).

COPULATION: (GFA)

NEST: Large, well-built structure of grass, seaweed and flotsam. Males fetch and 'present' nest-material, holding it in bill during some of display described above.

EGG/CLUTCH: $61.37 \pm 3.28 \times 37.35 \pm 1.46$. Weight calculated 46.1 g. Clutch varies between years. Ugaiushak Island 2.12 ($n=32$) one year, 3.08 ($n=49$) the next; Semidi Islands 2.5 (Nyeswander 1986); Pribilofs 2.84 (mean) varying with year and locality 2.62–3.0 (Hunt *et al.* 1981). Highest modal clutch, 4.0 on Ugaiushak (37% of 51 nests) mean that year 3.1 (Wehle 1978).

REPLACEMENT LAYING: No details.

INCUBATION: Shared; lasts 31–2 days (26–37).

CHICK/BROOD: Naked hatchling purplish with pale gular area. Soon clothed in dusky down tipped

with brown; paler on abdomen and white down elsewhere on underparts. Whitish area on outer thighs. When part-grown shorter, paler down replaces first covering; juvenile feathers begin to appear. Brood-size often quite low; 1.2–1.4 fledged young per nest known to have had eggs, but considerable variation between localities and years.

CARE OF YOUNG: Shared.

BEHAVIOUR OF YOUNG: No details.

FLEDGING: Presumably needs to develop adequate flight before venturing off cliff-ledge. Crèches usually impracticable? Fledging period *c.* 59 days (54–64) (Hunt *et al.*) though Nysewander estimated 49–50 days.

POST-FLEDGING: No details.

BREEDING SUCCESS: Hatched from laid: 25–46% (Pribilofs). Fledged per nest built: 0–1.91 (5 Alaskan areas, latter figure, if some nests never contained eggs, highly productive). Fledged from nests with incubated eggs: 1.25 (1.2–1.45) (Pribilofs). Although one report considered importance of human disturbance on these rather low figures (particularly some of the hatching successes) to be less significant than anything except storm-damage, it seems curious that supposed cause of greatest loss (predation by gulls) could operate on completely undisturbed cormorants. Corvids can be significant predators following disturbance. These two predators (glaucous-winged gulls and ravens) said to have caused failure of 81% of nests at Ugaiushak Island, which, in absence of disturbance, would be incredible. On Pribilofs, desertion considered most important, cause not stated but hunting by Aleuts implicated.

FIDELITY TO COLONY, SITE, AND MATE: Fidelity to colony and therefore to nest-site and mate, not strong, latter probably usually for one season only.

AGE OF FIRST BREEDING: Likely to be 3 years.

NON-BREEDING YEARS: Apparently not regular.

LONGEVITY AND MORTALITY: No information.

Rock Shag *Phalacrocorax magellanicus*

PLATE 7

Pelecanus magellanicus Gmelin, 1789, Tierra del Fuego and Staten Island.

Sometimes placed in *Stictocarbo* or *Leucocarbo*. Number of specific names (Murphy 1936).

Other common names: rock cormorant, Magellanic shag/cormorant.

French: cormoran de Magellan, cormoran Magellanique. German: felsenscharbe.

Spanish: cormoran Magellanico, cormoran de las rocas.

Description

ADULT M PRE-BREEDING: Head and neck black with blue gloss becoming purple with scattering white filoplumes continuing onto upperparts. Small but distinct white patch or tuft on ear coverts and wispy greenish median crest with longest feathers c5 cm. Upper back and wings dark with bottle green gloss and indistinct black margins to feathers. Lower back, rump, thighs and upper and under tail-coverts blue-black with plenty of white filoplumes. Tail black. Underparts white. Eye red-brown (breeding) to whitish; orbital ring, face and gular skin red, face bearing yellow papillae and bordered with black. Bill blackish. Legs, feet pink.

FEMALE: Similar.

POST-NUPTIAL: Lacks crest and white filoplumes. Throat, foreneck flecked white though doubt about whether this winter plumage or variants of breeding plumage.

JUVENILE AND IMMATURE: Dark brown head, neck, back, wings, tail, paler on upper breast, flanks, thighs and white or variably black or mottled on lower breast and underparts. Eye brown, legs, feet black. Immature green-glossed brownish-black on head, neck, breast and upperparts

acquiring small white filoplumes on head and neck. Brown on belly becoming whiter with age, as throat also whitens. Eye brown or pale, changing yellowish to pink, then red. Pre-definitive plumage said to be polymorphic (Rasmussen 1987). Legs, feet black changing to flesh as matures.

Field characters

Distinctive characters, white ear patch and combination of pink feet and blackish bill. Has weakest, least-hooked bill of South American cormorants. Wings exceptionally rounded; 2nd, 3rd and 4th primaries from outermost almost equally long whilst 5th about as long as first. Murphy notes flies low over surface and considers flight relatively weak, neither sailing nor soaring but beating steadily, with head a little lower than neck.

Measurements (see Appendix)

Voice

Low croak and 'clicking' in display.

Range and status

Breeds on Pacific and particularly Atlantic coasts of southern South America, including Tierra del Fuego and Falklands, extending N to Valdivia in Chile and Punto Tombo, Argentina. Vagrant further N. Far smaller population than imperial shag over most of range in Chile (A. Kepler personal communication). In Chubut Province (Argentina) c. 1,800 pairs in 27 colonies (Punta and Saravia 1993). Schiavini and Yorio (1995) give location and size of colonies in Beagle Channel (Tierra del Fuego). Falklands hold c. 1,000+ breeding pairs in 34 colonies, fewer than imperial (Johnsgard 1993).

MOVEMENTS: Largely sedentary, occasional vagrant further afield; seldom ventures far offshore.



6.127 Distribution of the rock shag. (After Johnsgard 1993.)

Foraging and food

Feed mainly near or over inshore kelp beds, evidently searching bottom in water mainly 1–6 m deep. Deep dives prefaced by upward leap and near-vertical descent. Wanless and Harris (1991) record dives lasted av 28 sec with 10 sec recovery periods, 1.8 dives per min. Feeding birds underwater 75% of time. Not surprisingly, dives lasted longer in deep water than in shallow. Adults took longer between long dives than short ones but juvenile recovery time independent of dive time. Consequently, in shallow water fully adult birds dived more often than juveniles. Presumably dive-and-search mode most efficient when done solitarily. Mean duration dive 47 ± 14 sec, surface interval 14 ± 6 sec ($n=11\ 212$ dives); diving efficiency (dive time/recovery time) highest recorded

for foot propelled diver (Quintana 1999, radio transmitters).

Fish appear to be main prey. Mulletts *Muligidae* and smelt *Osmeridae* thought to be important. In Argentina, *Ribeiroclinus* sp, *Patagonotothen* sp, *Agonopsis chilensis* and *Trathalassothia argentina* (Malacalza *et al.* 1997). Sizeable fish (up to 20 cm) may be taken, although apparently most prey only c5 cm long. Some invertebrates (crustacea, isopods, polychaetes), particularly in winter.

Habitat and breeding biology

(See Fig. at end of ch. 5; Siegel-Causey 1986b)

HABITAT: Preference for coastal channels and sheltered bays along rocky coastlines seemed to Murphy to correlate with weak flight. In Falklands frequents harbours, estuaries and inshore waters. Nests on top of steep-sided rocks or islets, on cliff-ledges or in gulleys, usually at least 6 m above sea; 90% Chubut colonies on rocky slopes mean 13.4 m from HWM (Punta and Saravia 1993). Sometimes nests in gloomy caverns so far back that only white breasts can be seen. In contrast to imperial cormorant apparently does not often use flat, open spaces. Occasionally uses artefacts such as jetty or wrecked ship.

COLONIES: Usually small and isolated (often <10 pairs); never large. Nests on ledges may be very regularly spaced. Same nest-site may be used year after year though not necessarily by same pair. Skuas often, Murphy says ‘invariably’, predatory attendants, stealing eggs and small chicks at change-over.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually. Arrives breeding area Aug. Tierra del Fuego, eggs found at least as early as late Oct giving well-grown young early Dec. Chubut (Argentina) nest building started 2nd and 3rd weeks Oct, eggs laid between 1st and 3rd weeks Dec (Punta and Saravia 1993) or last week Oct and 1st week Dec (Malacalza 1995). Chile, young found at least as late as April. Falklands, eggs from at least early Nov and young leave nest at least

as late as end of Feb. Sub-group differences in breeding chronology (Chubut).

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Sites defended by escalating sequence of threat. At lowest intensity bird 'stares', oriented towards opponent and with head and neck in line. Often incorporates sinuous snaking and head-shaking movements with increasing aggression. Tail raised, neck feathers erected and head darted at intruder, at high intensity gaping widely and croaking. Intermittently touches or worries nest-material.

Advertising males, usually standing with near-horizontal body, cocked tail and loosened wings, retracts head along mid-line and darts it forward and down, gaping slightly and 'clicking'. Gular area depressed. As female approaches he throws back his head until crown near base of tail, bill pointing upwards, and then rapidly and irregularly 'wing-flicks' 2–4 times per sec, in pulses. Gular still depressed and male vocalizes in synchrony with each wing-flick. Apparently does not rotate head after throwback. This display extremely similar to, and homologous with, its equivalent in other cormorants. Female approaches, gapes and may grasp or nibble base of his bill or gular area, or reach over his neck, but apparently nothing closely resembling mutual, side-by-side head-lowering of many blue-eyed shags. Mutual head-waving, initiated by either sex, involving reaching over other with throat-clicking; seems to be display described by Siegel-Causey as 'head-wagging'—reaching over with side-to-side head-movements. Nest-touching, throat-clicking and allo-preening (though not mutual-preening?) may be interspersed. At nest-relief incomer behaves much like female approaching 'advertising' male—lengthens neck vertically, head horizontal, and gapes. Nearing nest it throat-clicks, hops and vocalizes. Sitting bird may worry nest-material. Duration and precise sequence of these preliminaries to nest-relief not fixed but depends on motivation of both birds. Sometimes sitting bird may simply fly off.

In addition to threat and courtship displays, rock-shag, as other species, has ritualized its pre-take-off and pre-and post-landing behaviour. Before take-off may elongate neck, bill slightly downwards, and pulsate breast and abdomen.

When approaching occupied cliff-site, incomer calls 3–4 times and when some 3–4 m away throws up its webs, which are pink in contrast to black legs and toes, soles facing the site in clearly ritualized pre-landing gesture akin to that found in some other cormorants and boobies. Omits this when landing alone at unoccupied site. Post-landing posture resembles that of many other cormorants: head and neck extended horizontally, neck feathers erected and throat 'kinked'. Holding this position for a few seconds bird then slowly straightens up. Hop, too, is ritualized; a vertical hop with body upright, neck arched, bill pointing to feet and gular pouch depressed. Feet brought up in front of body. Finally, movement near nest is by ritualized locomotion, deliberate, high-stepping gait with neck at 45°, head and neck feathers erect, gular pouch depressed. Been interpreted as appeasement.

COPULATION: (GFA)

NEST: Largely seaweed but also tussock grass, leaves, twigs, and detritus cemented by mud and guano. Material gathered by male either on tide-line or by diving, female brings in small amounts until egg-laying. As with many cormorants male may place 'marker' of nest-material on his site before sexual advertising. After pair-formation he makes frequent trips with nest-material, 'presenting' it to female during post-landing display. Often pair handle material in concert, repeatedly placing it on rim. Nest often used year after year—not necessarily same pair.

EGG/CLUTCH: c62 (55.8–69.1) × 38 (36.5–39.8). Calculated weight 49.4 g. Clutch usually 2/3: 2.3 (Argentina, Punta and Saravia 1993); 2.0 (n = 28, Malacalza 1995).

REPLACEMENT LAYING: Probable (no details).

INCUBATION: Shared. Incubation period 28–30 days. Some loss of eggs to skuas during change-over on nest.

CHICK/BROOD: Hatchlings black, then covered in clove-brown down which later acquires variable

amount of white on belly. First true feathers brown above, tinged greenish, white on breast and belly sharply separated from brown upper breast and neck. Brood 2–3; no details on brood reduction if it occurs.

CARE OF YOUNG: Shared. No special features.

BEHAVIOUR OF YOUNG: No details.

FLEDGING: No details. Fledging period and post-fledging feeding not described but likely to resemble imperial shag.

BREEDING SUCCESS: 50% nests produced some fledged young (Malacalza 1995).

FIDELITY TO COLONY, SITE, AND MATE: Same general locality may support nesting group year after year but degree of fidelity of individual to precise area or to actual nest site not known. Mate fidelity not known.

AGE OF FIRST BREEDING: Unlikely to be more than 2 or 3 years.

NON-BREEDING YEARS: No information.

LONGEVITY AND MORTALITY: No information.

Guanay Cormorant *Phalacrocorax bougainvillii*

PLATE 7

Carbo bougainvillii Lesson, 1837, Chile.

Alternatively placed in *Leucocabo*.

Other common names: guanay shag, Peruvian cormorant or shag, Bougainville's cormorant. French: cormoran de Bougainville. German: guanoscharbe. Spanish: cormoran guanay.

Sub-species

Monotypic. Most closely related to cormorants of sub-Antarctic; has followed Humboldt N to within 6° of equator.]

Description

ADULT M PRE-BREEDING: Head, neck, back, wings and tail dark, glossed green (on head) or blue-green (back), bronze green (scapulars and wing-coverts) and greenish-black (quills and tail). Underparts white from base of foreneck to dark undertail coverts. Small erectile crest on forehead, white patch in mid-foreneck, white filoplumes above eye and others scattered about neck. Eye dark brown with white corneal ring surrounded by olive-green orbital ring; red facial skin which turns to orange above eye. Bill brown/black or yellowish, faintly pinkish or blue at base of mandible. Gular sac brownish. Legs, feet flesh or pink.

ADULT F: Similar.

POST-NUPTIAL: Adults lose facial plumes and oily gloss, giving browner tone overall.

JUVENILE AND IMMATURE: Juvenile markedly duller than post-breeding adult, brown beneath. Immatures and sub-adults similar to post-breeding adults but browner, with more white on foreneck.

Field characters

A large cormorant, long-billed, long-winged, bicoloured and crested, with white throat patch and green eye-ring. Differs from neotropic at all ages by having red face and white underparts and from rock shag by being bigger, with less extensive red on face, yellower bill, white on upper breast and foreneck.

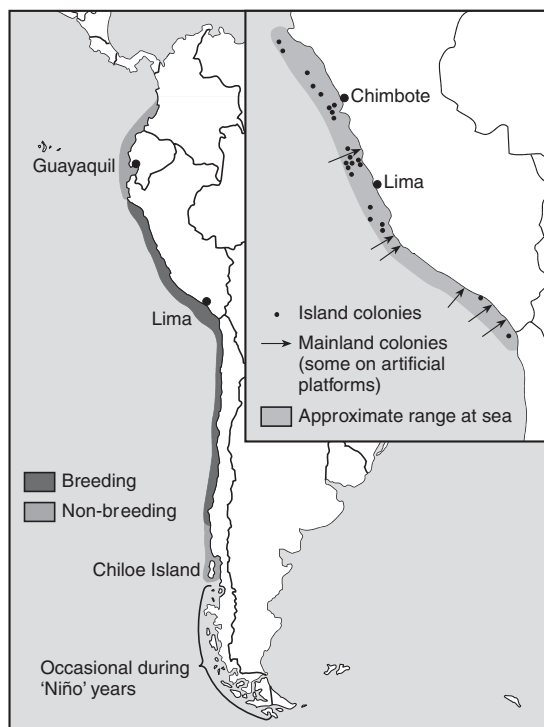
Measurements (see Appendix)

Voice

A huge colony makes a roaring gabble that overwhelms the ears; in Murphy's words 'oppressive roarings' and 'outlandish babble'. Individual calls are sonorous 'aarks' and higher-pitched screeches.

Range and status

Breeds on islands and headlands along Peruvian coast from just S of Gulf of Guayaquil through



6.128 A Distribution of the guanay cormorant. (After Johnsgard 1993.) Inset B Its main colonies. (After Nelson 1978b.)

Chinchas and Lobos islands to Chile, S to Concon Island near Valparaiso; c. 4,000 km. Colony at Mocha Islands now, apparently, extinct. Also on Atlantic coast of Argentina between Puerto Deseado and Santa Cruz. Non-breeders range further N and S.

Guanay population fluctuated enormously in both long and short term. Since pre-Incan times deposits on guano islands of Peru used as fertilizer and guanays one of 3 main guano birds alongside pelicans and Peruvian boobies (see Coker 1919; Murphy 1925, 1936; Vogt 1942, Hutchinson 1950, Nelson 1978b). Once initial deposits, in places more than 100 m thick, removed, guano industry had to rely on increments of 2 or 3 seasons. Even then more than 30,000 tons from single small island. In 1853 c. 13,376,100 tons on Chinchas alone. All 3 guano birds always subject to periodic devastation in Niño years and guanays fluctuated between perhaps fewer than a million and 15–20 million birds.

Recovery from this periodic mortality usually rapid due to high productivity in normal years, but huge increase in commercial fishing for anchovies since 1950s reduced fish stock to such an extent that seabirds less able to recover from natural perturbations. In 1981 guanay numbered c. 3,000,000 birds, about 40% of c. 8,300,000 guano birds, including pelicans and boobies (Duffy *et al.* 1984a). This proportion, as well as absolute number, considerably less than in past. Guanay once by far most numerous of these three.

MOVEMENTS: Normally resident in breeding area. Mass emigration in severe ENSO, N to equator and S to Chile and even inland. Post-breeding dispersal S to Chile may be regular feature even in 'normal' year.

Foraging and food

A uniquely aerial forager. Scouts for fish, at first in small parties, by searching from air, quartering ocean and flying much greater distances to feeding grounds than do other cormorants. Notably long wings may be adaptation for this, especially helpful in flying against strong winds that blow perpetually off coast of Peru. When moving to distant feeding grounds, travel 'as a solid river of birds in an unbroken column close above the waves . . . a single formation taking four or five hours to pass a given point' (Murphy 1936). When shoal located dense rafts of cormorants form on sea, birds from rear of forward-moving flock continually rising and flying to front, 'pouring over the van'. Feed exclusively on surface-swimming fishes, mainly anchovies, (remains of 76 anchovies, each 10–12 cm long, taken from dead guanay) which is why they suffer so drastically when warm water in Niño year drives cold-loving anchovies inaccessibly deep. Murphy believed guanays had evolved efficient cooperation but more rigorous interpretation would not see it as such. Apparently, birds sally forth in small parties in morning and when they begin to feed, huge numbers may join them. But existence of a feeding flock visible in distance may have no effect in attracting a band leaving an island, nor does successful fishing operation of one day determine direction of flight next day. And no reason to suppose that birds

which locate shoal benefit from attracting others. Certainly no overt cooperation equivalent to that found in some pelicans. Intensely communal feeding may be inevitable consequence of huge numbers of fish and of birds. Similarly, feeding cormorants joined by gulls, pelicans, boobies, and sea-lions (guanays often have fish stolen from them by pelicans, which attack them once they have surfaced and are swallowing their catch). Occasionally fish trapped between predators and shore but not known to be an intended result. Birds usually leave roosting or nesting place c. 06.00–10.00 hr returning 12.00–18.00 hr but occasionally not until after night-fall. Occasional nocturnal excursions near full moon. Normally do not need to forage more than c2 hr a day, but when food short this period greatly exceeded. Vogt (1942) suggested that when guanays had to forage for long periods each day mass desertion would ensue.

Mean content of food in birds returning from fishing 143.2 ± 22.5 g (Vogt 1942) suggesting range between 76 and 211 g fish per day, but allowing for 50% digestion of catch during fishing (overestimate?) gives mean catch of 214.7 g and max 316 g, latter approximating quite well to intake of captive birds.

Habitat and breeding biology

(See Fig. at end of ch. 5; Murphy 1936; Hutchinson 1950; Duffy 1994)

HABITAT: Exclusively marine. Inhabits arid coasts and offshore islands, out to c30 km, mainly of Peru, washed by cool, rich Humboldt with its trillions of anchovetas. A more gregarious bird is beyond imagination.

COLONIES: Huge (Central Chincha has held >1 million nests) and extremely dense, c. 3 pairs per m² but up to 3.6. Distance between nests, centre–centre, c60 cm. Ground covered unbelievably thickly, yet new arrivals plump down by the hundreds. Vogt (1942) suggests guanays cannot breed successfully in colonies smaller than c. 10,000 birds (improbable; no known instance of such a high lower limit).

Breeding areas determined by temperature. Usually exposed to constant wind, which cools and facilitates landing among hostile neighbours. Max ground temperature in part of North Chincha colonized by guanays varied throughout breeding season from 27.5–42.5°C; modal max temperature 33.5°C (Vogt 1942). On side of island without birds max temperature 50°C mode 42.5°C. Hutchinson (1950) suggested primary factor determining breeding-sites is adequate exposure to wind. Colour of substrate may play a part; black sand of Isla Vieja may absorb too much heat for guanay to inhabit. Vogt claimed that avidity with which pre-fledgers of 6–7 weeks sought the water depended on amount of wind. Guanays said to prefer sloping, bare,



6.129 Guanay cormorants, Peru, nest in dense masses on arid slopes. The most crowded colonies of any cormorant.

rough rock rather than sand or pebbles or highly irregular ground. Tendency to change nesting locality from year to year may reduce infestation by parasites; guanays suffer greatly from ticks *Ornithodoros amblus* and mallophaga (feather lice), former leading at times to such massive anaemia that many birds die, though food-shortage also implicated. Avian cholera and aspergillosis can also cause heavy mortality, but above caveat may apply here, too. At a 'new' location for a colony, thousands of cormorants stand compactly, at first showing little courtship but rapidly increasing tempo. Even within such dense and ostensibly homogeneous masses sub-groups of birds synchronize their breeding. Colony tends to grow peripherally, outermost pairs less advanced than central ones. Establishment of breeding colony on one island apparently siphons off birds just ready to breed from other islands.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Although breeding may seem continuous, with pairs at all stages, no firm evidence that same pair breeds more than once a year. Nevertheless this has been claimed and remains possible; may be part of mechanism by which populations recover so rapidly after devastation during Niño years. Murphy says that individual pairs of guanays are believed to rear 2 broods a year. In normal times may lay in any month, but laying peaks Nov–Jan. Oct probably month when most pre-laying courtship occurs. Complete breeding cycle takes *c.* 4 months.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Competition for nesting space presumably severe and overt fighting occurs though not damagingly. Also lunges and snaps. Murphy remarks that quarrels ceaselessly and sometimes general mêlées.

Details of pair interactions lacking but resembles Antarctic cormorants, from which it derives. Extremely dense nesting presumably poses problems for unpaired males advertising and unpaired females prospecting, but perhaps most pair-formation occurs on periphery. Murphy refers to 'throwback' when he says they extend head upside down along spine 'holding this curious, paralysed attitude for several seconds'. Partners smooth heads and necks over each other and 'bill',

apparently snapping at and evading each other's head movements. They 'kink-throat', erect crest feathers and ruff out those of nape so that head and neck enlarged. Gape continually. However, several behaviours likely to be in their repertoire have not been described and detailed ethogram needed.

COPULATION: (GFA)

NEST: Almost entirely of guano with stones, detritus and moulted feathers. About 32 cm diameter and 17 cm high, although accumulated nests may consist of new one burying old. Site characteristics include slope of $c20^\circ$. This cormorant regarded most valuable bird in world because of commercial value of its guano. Vogt (1942) estimated that each m^2 of a colony laid down 96 kg per year, each bird producing 43.5 g per day, from fish intake of 300 g. Conversion ratio apparently leaves little margin for loss of guano at sea, implying that guanays retain it until at nest.

EGG/CLUTCH: $64\text{--}65.7 \times 40.7\text{--}41.6$ $n=2$. Calculated weight 60.3 g. Clutch 2–4, av 3.13 ± 0.1 .

REPLACEMENT LAYING: In normal years lost clutches replaced. In years of wholesale desertion, no replacement laying occurs.

INCUBATION: Shared and no unusual features described; period $c28$ days.

CHICK/BROOD: Hatchling black. Becomes covered with even mixture of black down and white down 'pepper and salt', apparently peculiar to this species (Murphy 1936). Brood 2 or 3. No information on slight brood reduction that must occur.

CARE OF YOUNG: Brooded for a time and after that, only at night. Parents not only shade them but according to Hutchinson (1950) sometimes 'fan' them with their wings; if true, a unique trait.

BEHAVIOUR OF YOUNG: Murphy records that at times 2 or even 3 young manage to enter adult's throat simultaneously. Chicks begin to roam before they can fly which may lead to attacks from

neighbouring adults. Later go down to rock pools in droves and bathe and dive, returning to colony before dark, though whether chicks from central nests can return there not clear and seems unlikely, since intervening adults attack them.

FLEDGING: See above; period probably *c.* 8 weeks.

POST-FLEDGING: Feeding occurs; period not recorded.

BREEDING SUCCESS: Oddly for such accessible and well-known bird, basic breeding biology imperfectly documented. Mean hatching success not recorded. Even in 'normal' (non-Niño) years, may be significant desertion. Over 69 'normal' years some desertion in 32 of them, commonly ascribed to infestation with ticks but possible role of disturbance not evaluated. Vogt suggested that if feeding takes up 6 or more hours a day, food is short and desertion likely. Murphy records 2–3 young per breeding attempt normally produced. Seems

condor only significant predator of 'undisturbed' nests, though gulls and turkey vultures take eggs and small young if adults disturbed. He gives graphic account of part-ravaged colonies which suffer particularly heavy losses at edges and on projections.

FIDELITY TO COLONY, SITE, AND MATE: Guanays frequently change breeding locations. Fidelity to site and mate highly unlikely to endure for more than one breeding cycle.

AGE OF FIRST BREEDING: Probably 2 years.

NON-BREEDING YEARS: Probably only when food fails.

LONGEVITY AND MORTALITY: Longevity unknown. Mortality not accurately known but in normal years unlikely to be higher than 10–15% annual adult mortality.

Pied Cormorant *Phalacrocorax varius*

PLATE 7

Pelecanus varius Gmelin, 1789, New Zealand.

Also referred to as *Hypoleucos varius*.

Other common names: greater pied, large pied, yellow-faced, black and white cormorant/shag, pied shag.

French: cormoran varié. German: elsterscharbe. Spanish: cormoran pio. Known to Maoris as karuhiruhi.

Sub-species

P. v. hypoleucos: mainly coast of West Australia; also inland; resident.

P. v. varius: coast of North Island, New Zealand but locally elsewhere (South Island, Stewart Island).

Description

ADULT M PRE-BREEDING: Large cormorant, black above, white below. Crown, back of neck, whole of upper parts including tail and thighs blackish.

From slightly above eyes through cheeks, sides of neck, chin, throat, all underparts white. Back glossed green or bronze, feathers bordered black. Patch of wrinkled skin, yellow or orange, in front of eyes. Throat, angle of gape salmon pink. Eyes green with brilliant blue orbital ring. Bill grey with dark ridge. Legs, feet blackish. Marchant and Higgins (1990) note that some birds (less than 1%) resemble blue-eyed shags (*atriceps-albiventer* group) in having white patches on upperwing and scapulars and white line along upper arm bone area of underwing. They record that 2 sub-species differ: *P. v. varius* has smaller patch of skin on lores; black feathering on nape intrudes into white neck; mid-throat feathers extend further forward than in *P. v. hypoleucos*; black/white border on side of head starts at eye-level rather than above eye as in *hypoleucos*, sheen on back green rather than the blue of *hypoleucos*.

ADULT F: Similar but smaller, especially bill.

POST-NUPTIAL: Upperparts fade to dark brown with sandy edges to coverts. Face becomes yellow and eye-ring paler.

JUVENILE AND IMMATURE: Dark brown upperparts well demarcated from streaky white and brownish ventral surface, brown often forming noticeable pectoral band. Some juveniles entirely brownish beneath. All have brown cheeks. Bill pinkish or greyish with dark culmen. Face creamy, eye-ring grey and eye dark brown. Immatures variably mottled dark and light brown above and white and pale brown beneath, brown usually confined to upper breast. Gives way to adult plumage in 2nd year.

Measurements (see Appendix)

Voice

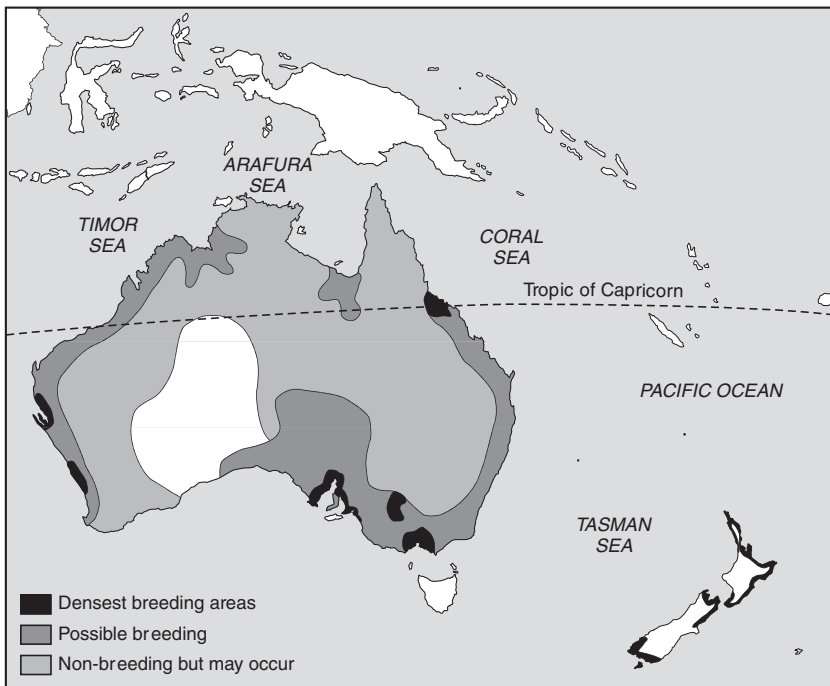
Male has sonorous 'aark' and more variable and staccato disyllabic calls associated with display during breeding; whistling 'prit-prit', rick-tick-tick; 'kerlik' which run together. Colonies noisy during breeding. Females hiss. Chicks utter food-begging

call, 'whee-whee' or chirrup for first 3 weeks and thereafter a threat call—a harsh 'a-aark' which males retain throughout life but females lose at 5–6 weeks; virtually silent after fledging.

Range and Status

(Marchant and Higgins 1990)

Widespread but discontinuous in Australia and New Zealand (endemic). Coastal and offshore islands of W and S Australia and inland, except for driest areas *c.* 120–33° E to 20–30° S. Recently extinct Tasmania. In New Zealand occurs North Island from North Cape to Auckland and along E coast and on South Island from Cape Farewell to Christchurch and Milford Sound to Invercargill and on Stewart Island. Straggles to the Snares. Most plentiful from Cape Maria Van Dieman to Waikato River mouth. Also Motueka to Banks Peninsula, Milford Sound to Nugget Point and on Stewart Island; estimated population 5,000–10,000. Although conspicuous, total population not great. In total New Zealand may hold



6.130 Distribution of the pied cormorant. (After Johnsgard (1993) and Marchant and Higgins (1990).)

fewer than 100,000 birds and although Australian population not estimated, small size of vast majority of colonies, sparsely distributed, suggests moderate numbers.

MOVEMENTS: Largely sedentary; some juveniles disperse. Only 7% ringing recoveries from S Australia occurred outside immediate area (van Tets *et al.* 1976). Beach recovery rates in New Zealand change significantly through year; most Nov–March, when most fledged young are around. However Marchant and Higgins state that some places—e.g. Victoria—report rate constant throughout year. Possible positive correlation of numbers with rainfall in, e.g., Queensland.

Foraging and food

Marchant and Higgins (1990) summarize prey species. Flies between roosts or colonies and feeding areas singly or in groups, sometimes in V-formation. Begins foraging an hour or two after sunrise and ceases an hour before sunset though may leave roost before sunrise. Prefers to feed singly but will gather in large numbers over shoals. Feeding segregation suggested to minimize competition when feeding with other species but great cormorant must overlap very significantly where these two occur together. Feeds on bottom in water typically 3–10 m deep and dives for c25–60 sec in deeper water; 10–20 sec in water 1–2 m. Pollutants in food, as at sewage farms, may cause deformities in nestlings. Typical prey 10–30 cm and up to 600+ g, mainly fish but cephalopods and crustacea locally important. Depends heavily on certain species in some habitats but markedly opportunistic. In estuary in W Australia ‘perch’ *Apogon* sp nearly half prey ($n = 2652$, 160 cormorants). Gobiids also important (*Glossogobius* 18.6%, *Arenigobius* 12.7%). Food intake adults < 500 g per day; max intake large young c600–800 g per day.

Habitat and breeding biology

(See Fig. at end of ch. 5; Millener 1972; Norman 1974; Marchant and Higgins 1990)

HABITAT: Chiefly marine coastal—lagoons, estuaries, rocky shores. Inhabits, also, interior wetlands such as swamps, rivers, and deep lakes as well as

artefactual waters such as reservoirs and sewage ponds. Often mixes with other cormorants and waterbirds. Prefers open stretches to shallow, densely vegetated waters but tolerates wide range of depth, salinity and turbidity. Nests on cliff-tops, offshore islands (though usually not on bare rock or earth), and inland in trees or bushes especially where these emerge from standing water. Often kills trees by fouling them and plucking twigs for nest-material.

COLONIES: Vary greatly in size, from <10 to >1000; typically 10–20 pairs. Sometimes breeds in mixed colonies containing little pied, little black or great cormorants. Typical cormorant habit of often changing site of colony between successive breeding attempts—attributed to having killed trees but an insufficient explanation. As an essentially sedentary species except for juvenile dispersal, colonies not subject to marked immigration and therefore fluctuate little in size from year to year.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Appears to breed annually. Total length successful breeding cycle c21 weeks, varying with region. Laying recorded in all months with peaks in autumn and spring in coastal areas though probably involving different birds. Overall, autumn laying may be favoured.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: (van Tets in Marchant and Higgins 1990; Millener 1972): overt fighting rare. Males settle on potential nest-site; defended by ritualized threat—sinuous darts and twists of head. Bill open or closed, gular pouch expanded or not and feathers of head and neck variably raised. Accompanied (males) by loud, harsh vocalization and (females) sibilant hiss. Displacement activity (nest-touching or worrying) interspersed.

Males advertise using typical cormorant wing-flicking display oriented towards potential mate. Partly folded wings flicked upwards 1–2 times per sec whilst tail and rump raised and head rested on back, bill pointing upwards. Silent. After period of wing-flicking male throws head back beyond vertical, though not flat along back and not rotated, then

brings it forward again, bill open, and vocalizes—‘screech’. Closes bill and depresses hyoid. During this forward movement rotates head and ‘gargles’ or ‘barks’. This part of display—so-called ‘gargling’—used by both male and female (female hisses) as a ‘recognition’ display. Thus male precedes it by wing-flicking when he is advertising, but not after pair-formation, when he is ‘recognizing’, and female, who does not need to advertise, uses it solely as recognition, without wing-flicking. Often, at end of this display, head and neck remain extended ‘pointing’ with tail at less of an angle than before. In one version of ‘pointing’ both partners, one on nest and other alongside, face same way with closed bills pointing slightly upwards. Mate’s arrival at nest stimulates ‘gaping’, in which head, with widely opened bill is moved forwards and backwards with bent neck and depressed hyoid. Male vocalizes but female silent. Before take off from site, assumes upright, elongated posture with bulging throat and pulsation at base of neck as bill opens and closes in synchrony with a ticking sound (male only). Before and accompanying landing, as far as 100m from site, bird ‘kink-throats’ and (males) vocalizes (a whistling) in time with wing-beats. After landing, silently assumes conspicuous ‘discoidal’ head and may retain it during hop, a sizeable jump with feet together and wings, head and neck motionless, usually ending with a gape. This ritualized hop characterizes movement around site and mounting-dismounting during copulation. These pre-departure, post-landing and on-site-movement postures and (male) vocalizations are elicited by courtship habit of ‘circle-flying’—short flights out from and back to nest site, which probably condition partners to departures and returns. May allo-preen after mating and perform many of displays described above.

Seems female selects mate; may visit and leave several though basis of rejection obscure. Correspondingly male may advertise to several females only to reject one who approaches. In this case it may be that he has already formed a pair-bond but that, nevertheless, advertising display had been triggered by presence of females.

COPULATION: (GFA)

NEST: In trees, bushes, rarely bare ground. May be lightly built; readily displaced by high winds. Male

collects most material (twigs, vegetation, seaweed, flotsam). Both sexes build, taking *c.* 3 weeks but enormously variable; *c.* 45 cm across base, 30 cm at top, up to 45 cm high. Material added during incubation and chick-rearing.

EGG/CLUTCH: Australia: 59 (54–62) × 38 (34–40) *n* = 24; 60 (55–67) × 38 (34–40) *n* = 23; 58.9 (51.9–60.3) × 38.7 (35.9–48.5) *n* = 47. New Zealand: 59 (53–68) × 38 (35–41) *n* = 315. Clutch usually 2–4 occasionally 5. Of 256 clutches, 7 contained 1 egg, 24 (2 eggs), 107 (3), 116 (4) and 2 (5), *av* 3.32. Eggs laid *c.* 2 days apart; synchronized within sub-groups.

REPLACEMENT LAYING: Occurs, but no figures.

INCUBATION: Shared about equally. Even before eggs laid partners regularly change-over on nest. During change-over ‘in’ bird gapes and worries nest-material. Changes over at least 3 times a day during incubation and until chicks *c.* 3 weeks. Incubation period: Egg 1 28.5–33 days; egg 2 27–31.5; egg 3 25–29.4; egg 4 25–8.

CHICK/BROOD: Hatchling pink becoming black. Down dark brown above, paler below. Face yellowish, bill pale cream. No details differential survival of differently aged siblings.

CARE OF YOUNG: At least one parent attends young until *c.* 4 weeks old. Even after that, unattended young, average age *c.* 6 weeks, may be displaced by intruding adults and subsequently abandoned by parents—unusual among cormorants. Parents said to shade chicks from sun and shelter them from rain by extending one or both wings above them in appropriate direction. Odd that such an adaptive habit largely absent in pelecaniforms, especially if present in some. Regurgitation preceded by kink-throat. When chicks very small parent appears to stimulate them and proffers pre-digested food. Older chicks kink-throat when begging which, after *c.* 2 weeks, is vigorous with wing-flapping. Feed offspring up to 6 times per day, decreasing to 1–2 near fledging. Parents preen chicks but not vice-versa.

BEHAVIOUR OF YOUNG: Able to sit on tarsi from *c.* 2 weeks. At 4 weeks can sidle along branch and at 5 weeks walk and perch like adult. May crèche

when in ground colony and even when in tree may leave nest at this stage. Begging of larger young side-to-side head movements and pestering contact with adult's bill, repetitive vocalization, bill closed, depressed hyoid. Siblings compete strenuously for food but siblicide not recorded (siblings may preen each other). Male young aged 10 weeks may perform version of adult's advertising and greeting displays, uttering harsh 'a-aark' calls.

FLEDGING: Chicks said to leave nest at *c.* 4 weeks (undisturbed?). Can they do this in trees? Seems very early. Fledging period 47–60 days, former presumably not sustained flight.

POST-FLEDGING: Fed until young *c*80 days, sometimes much longer (up to 133).

BREEDING SUCCESS: (Norman 1974) Hatched from laid: 43.3% (*n* = 511 eggs). Fledged from hatched: 60.6%. Fledged from laid: 26.2%. This unusually low figure unlikely to be representative of undisturbed birds. Even 3-egg clutches, most productive clutch-size, managed only 45% hatching success. Fledging success, however, quite high. 83.3% of young, hatched from 2-egg clutches, succeeded in fledging but sample (12 clutches) small. Millener's (1972) New Zealand study concluded that broods which hatched most synchronously were most successful

and this factor more influential than brood-size. Presumably where chicks more or less equal, competitive exclusion of any of them less likely. Main cause of failure appeared to be human disturbance leading to loss of eggs or young, and human 'culling'.

FIDELITY TO COLONY, SITE, AND MATE: Apparently tends to return to natal colony (more likely to be to general natal area than to precise colony) after variable dispersal. As in other cormorants, fidelity to precise location of colony not strong; colonies tend to move within a general area. For example, on Carnac Island (W Australia) breeding pairs remained *c*450–550 but bred on different part of island each year (Wooller and Dunlop 1981). Therefore fidelity to particular breeding-site cannot be long-term. Fidelity to partner highly unlikely, too, although if site happens to be maintained for successive breeding attempts pair-bond, also, may well endure.

AGE OF FIRST BREEDING: May pair at 1 year but no effective breeding until at least 2.

NON-BREEDING YEARS: No information.

LONGEVITY AND MORTALITY: Not known. Unlikely to differ greatly from other cormorants.

Black-faced Cormorant *Phalacrocorax fuscescens*

PLATE 7

Hydrocorax fuscescens Viellot, 1817, Tasmania.

Sometimes placed in *Leucocarbo* or *Campsobalieus*.

Other common names: black-faced shag, black-and-white shag/cormorant, white-breasted cormorant.

French: cormoran de Tasmanie. German: Tasmanien-kormoran. Spanish: cormoran carinegro.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Head, hindneck, back, flanks, and thighs black with blue or green gloss, black on crown extending down to just below eye

though sloping slightly upwards to join back of crown. Wing-coverts and scapulars trifle more greenish, former with conspicuous whitish margins. Tail and wings blackish. Underparts white from vent to chin, including sides of neck and broad white cheeks. Lores barish and covered with small white papillae. Scattered white plumes on hind-neck, back, and flanks. Eye dark blue-green, eye-ring and face purplish black. Bill stout and slaty black, sometimes greenish. Gular skin, legs, feet black.

ADULT F: Similar.

POST-NUPTIAL: White plumes lost though white filoplumes remain.

JUVENILE AND IMMATURE: Juvenile blackish-brown on back with lighter borders to feathers; essentially streaky below with white feathers tipped with shades of brown. Tail, wings, thighs black-brown. Crown, hind-neck black-brown with greenish gloss. Short white filoplumes on nape. Throat, sides of head white, tipped dark brown. Iris pale greyish, gape creamy brown. Upper mandible grey-brown, lower cream to light brown. Eye-ring light brown. Legs black. Immature bird acquires more of green gloss on upperparts, loses streakiness on neck, sides of face, underparts.

Field characters

Marine or estuarine; medium-sized, black and white shag of coast of South Australia. Differs from more widespread pied cormorant in facial pattern, demarcation between black and white starting above eye in pied, giving white-faced appearance compared with black face of *fuscescens*. And face yellow in pied but dark in black-faced. This last characteristic helps to separate juveniles, too.

Unlike other Australian cormorants holds head low in sustained flight (Serventy *et al.* 1971)

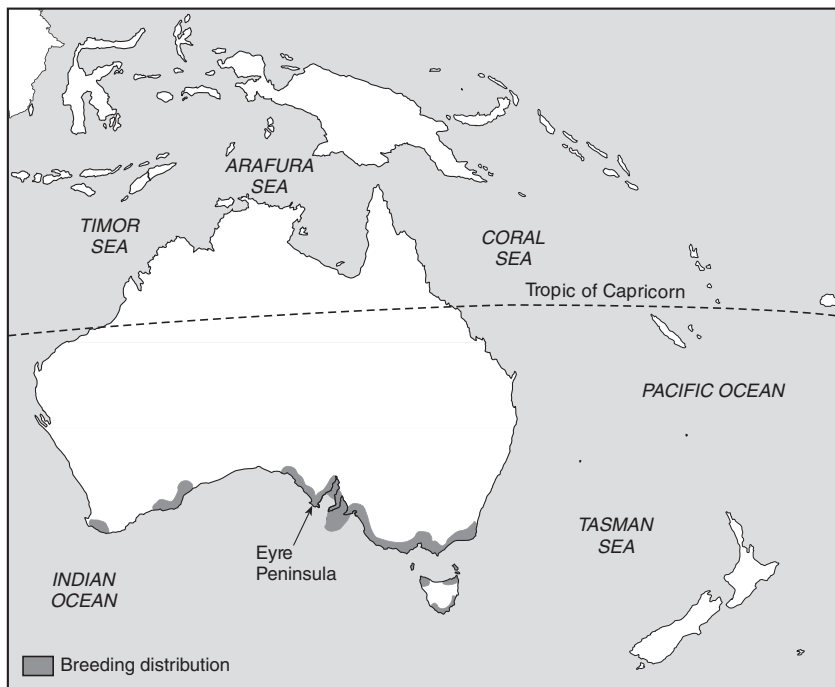
Measurements (see Appendix)

Voice

Threat call 'aarhg-aarhg'; in display (throwback) 'ah-woo'; during kink-throating and gaping a repeated 'huck-huck' or 'ah-ah, ah-ah'. Before take-off a single or multiple clapping ending with mechanical snap and, sometimes, soft ticking.

Range and status

Endemic Australia; confined to S coast (Hopetown, W Australia, eastwards to Israelite Bay then Seduna eastwards into Victoria) along with Bass Strait Islands and Tasmania (Serventy *et al.* 1971). Populations in E and W of Australia apparently separate (Marchant and Higgins 1990). Numbers may be declining and range contracting, probably mainly due to persecution. Largest colonies occur off Eyre Peninsula, totalling c. 5,000–10,000 pairs in 1970s and 1980s. In Tasmania largest



6.131 Breeding distribution of the black-faced cormorant. (After Marchant and Higgins 1990.)

colonies, several hundreds, in Furneaux group. Elsewhere, colonies small.

MOVEMENTS: Generally sedentary; young birds may disperse some hundreds of km.

Foraging and food (McNally 1957)

Marine and estuarine inshore waters, rarely in inlets or bays (some authors), 'forages in bays and inlets'; occasionally up coastal rivers. May feed solitarily or in flocks of thousands, birds said to cooperate though method not described. Typically forages in shallow water (up to *c.* 12 m) especially over reefs, dives 20–40 sec. Unlike many cormorants which have 2 feeding periods each day, said to forage only once, consuming *c.* 20% of their weight; which improbably high. Pebbles swallowed as ballast. Fish include Atherinidae, Scorpaenidae, Syngnathidae, Platycephalidae, Callionymidae. Largest prey *c.* 50 cm.

Habitat and breeding biology

(See Fig. at end of ch. 5; some details Marchant and Higgins 1990)

HABITAT: Cliff-ledges, in clefts, or on tops of bare rocks, just above HWM—*c.* 100 m. Sometimes in vegetation; rarely, sandy islands.

COLONIES: Nests solitarily, in groups of 2 or 3 or larger, up to *c.* 3,000. May nest alongside pied cormorants, gulls, or terns. In densest colonies nests no more than *c.* 1 m apart but spacing highly variable. Some colonies, such as particular island, highly permanent, but probably not tied to specific areas within that locality.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Not known to breed more than once a year. Apparently breeds all-year-round over range as whole but probably broadly seasonal peaks in particular localities such as Tasmania and S and W Australia. Much incubation Aug–Jan.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Male establishes site. Both sexes defend by threat-gape, moving head backwards and forwards and sideways with irregular, sinusoidal neck

movements. Throat bulges. Body horizontal, wings held out and down, tail fanned and raised. Head and neck enhance visual impact by raising feathers below prominent nape-line, imparting broad, ruff-like appearance.

Male advertising display silent, head and neck feathers sleeked, tail cocked. Neck held in tight S curve with head almost touching back and closed bill pointing obliquely upwards. Tips of partly opened wings flicked upwards and outwards *c.* 4 times per sec, very rapid compared with other cormorants—typical of way in which homologous displays diversify. In throwback body switches from horizontal to upright and head swings back through vertical arc until nape touches rump, but head not rotated. Sometimes gargling 'ah-whoorr' uttered, first syllable as head swings back with bill open, second with bill closed as head touches rump. So-called recognition display resembles threat directed at rivals in that gaping bill directed forwards and upwards with vocalization (males) or soft hiss (female). May then progress into formal 'throw' of head which terminates with mechanical snap of bill and (males) clattering or grunting call.

Exhibits typical range of postures at nest-site—pre-take-off, pre-hop, post-landing and post-hop, characterized by vertical body posture with hunched and horizontal head, closed bill, distension of tongue bone and erection of plumage of nape and hind-neck. In pre-take-off posture males may 'tick'. Arrival at site accompanied by kink-throating with closed bill and (males) repeated calling.

COPULATION: No details.

NEST: Large; 40–50 cm outside diameter and 7–18 cm deep, of seaweed and flotsam, lined with grass. Male brings nest-material which female builds. Continues during incubation and chick-rearing.

EGG/CLUTCH: 58.8 (57.7–59.9) × 37.4 (34.8–39.4) *n* = 9; 59.1 (54.9–63.5) × 35.8 (34.3–37.8) *n* = 7; 57 (59–61) × 36 (33–8) *n* = 1. Clutch usually 2–3, occasionally 4, even 5.

REPLACEMENT LAYING: No details.

INCUBATION: Shared; period not recorded.

CHICK/BROOD: Hatchling naked and black. First thick down woolly and black-brown with scattered white mesoptiles. Face and throat pinkish only sparsely covered with dull white down; white (pepper and salt) below. Gular pouch pale yellow. Legs and feet grey. Thighs dark brown. No details of development. No information on commonest brood-size, reduction, etc.

CARE OF YOUNG: Shared; no unusual features.

BEHAVIOUR OF YOUNG: During begging, pouch distended (large and yellowish from front); chick said to peck at parent's neck. Several young may importune returning adult but no evidence that adult feeds other than own. Apparently may form crèche.

FLEDGING: Precise age not recorded, but young prone to leave nest quite early in development particularly if disturbed. May be fed whilst on water.

POST-FLEDGING: Period of feeding unknown but does occur away from nest.

BREEDING SUCCESS AND OTHER ASPECTS OF LIFE CYCLE: Little studied species.

Blue-eyed Shags

Introduction

Members of a circumpolar group of southern-hemisphere shags, especially around southern tip of South America and in sub-Antarctic and around New Zealand, are closely related and difficult to pigeon-hole as a species with sub-species or a super-species with species. Murphy (1936) offered first detailed discussion and Devillers and Terschuren (1978) provide well-referenced summary; see also Voisin (1973). 'Blue-eyed shags' often assigned to *atriceps*, *albiventer*, *carunculatus* with usually *campbelli* in addition; recently, however, greatly subdivided. Marchant and Higgins (1990) following Peters (1931) place 13 species within *Phalacrocorax*. Del Hoyo *et al.* (1992) also use generic *Phalacrocorax* and embrace 13 species (though not exactly same list). Johnsgard (1993) sheds traditional allegiance to *Phalacrocorax* and uses *Leucocarbo* (after Siegel-Causey 1988). He recognizes 9 species but uses trinomial

nomenclature to accommodate remainder. He gives Pitt shag specific status but relegates *albiventer*, *bransfieldensis*, *georgianus*, *nivalis*, *melanogenis*, *verrucosus* and *purpurascens* to races of (*Leucocarbo*) *atriceps*. Devillers and Terschuren use trinomials to divide *atriceps*: *P. a. atriceps*, continental S America, polymorphic; *P. a. albiventer*, Falklands; *P. a. melanogenis*, Crozet, Marion, Prince Edward Islands; *P. a. purpurascens*, Macquarie; *P. a. georgianus*, S Georgia; S Orkney, S Sandwich; *P. a. bransfieldensis*, Antarctic peninsula, S Shetland, Elephant Island; *P. a. nivalis*, Heard Island. Siegel-Causey, comes up with 4 genera and 12 species and Van Tets (1976), using behavioural criteria, arrives at 9 species.

Kernel of blue-eyed shag group is *atriceps*/*albiventer* duo which may derive from an ancestral *carunculatus*, the group gradually moving eastwards assisted by westerly winds and prevailing currents (Voisin 1973). 'The forms formerly grouped in *atriceps* and *albiventer* give rise to *atriceps* (incorporating *albiventer*), *bransfieldensis*, *georgianus*, *nivalis*, *melanogenis*, *verrucosus* and *purpurascens*; *chalconatus* and *onslowi* are separated from *carunculatus* and *campbelli* is divided into *campbelli*, *colensoi* and *ranfurlyi*' (del Hoyo *et al.* 1992).

The common names are like myriad footprints criss-crossing in the snow and about as easy to disentangle. *Atriceps* has been called: imperial shag or imperial blue-eyed shag; emperor shag; king shag (given specific name *albiventer* by those who do not subsume *albiventer* under *atriceps*); Antarctic (sometimes called the sub-Antarctic shag and usually given specific name *bransfieldensis*); Magellanic blue-eyed; Falkland blue-eyed (specific name *albiventer* by separatists); Georgia or Georgia blue-eyed *georgianus*; Heard *nivalis*; Kerguelen *verrucosus*; Macquarie *purpurascens*. Some are sometimes called cormorants rather than shags.

Rasmussen (1994), examining populations from seven South American localities, discusses in detail the hypothesis that Pleistocene glaciations in South America led to differentiation in the imperial shag (*P. atriceps*). Size of alar bar, crest, and white dorsal patch vary geographically in juveniles but not adults. Differences between populations in skeleton are marked, particularly in males. Birds from the lowest latitude in central Chile have comparatively long culmens. There are significant morphological differences

between lake and coastal populations. In Chile these shags were probably not isolated for long, because they can breed on unglaciated headlands. Rasmussen supports treatment of

the Falkland Islands population as a distinct subspecies. Populations from the southern Atlantic coast and Tierra del Fuego were probably contiguous during the Pleistocene and differ only clinally in size.

King Shag *Phalacrocorax carunculatus*

PLATE 9

Pelecanus carunculatus Gmelin, 1789, Queen Charlotte Sound, New Zealand.

Now placed by some in *Leucocarbo* or *Eleucorbo*.

Other common names: Marchant and Higgins 'king shag'; 'rough-faced' 'carunculated' shag or cormorant (del Hoyo *et al.* 1992). Occasionally Cook Straits or Marlborough Sound shag or cormorant, and New Zealand king shag.

French: cormoran carunclé. German: warzenscharbe. Spanish: cormoran carunculado.

Sub-species

Some authors have included *chalconotus* and *onslowi* as sub-species of *carunculatus* (e.g. Dorst and Mougín 1979) whilst Peters (1931) included several others, too, but his grouping not now accepted.

Description

ADULT M PRE-BREEDING: Metallic blue-black of head and hindneck starts at side of chin making entire head appear dark. Black crest on forehead. Back dark purple-brown with green sheen and indistinct black borders to feathers. Tail black. Scalloped white alar and scapular patches variably conspicuous or even absent. Pair of white patches on back prominent in some birds. Chin, throat, foreneck and rest of underparts white. Underwing black with white along humeral area. Bill grey-pink with pair of orange caruncles above base. Face and gular area blue-grey, eye-ring blue. Inside mouth red. Eye hazel. Legs and feet pinkish-grey.

ADULT F: Similar.

POST-NUPTIAL: Loses crest; soft parts and dorsal plumage fade and caruncle becomes dull yellow.

JUVENILE AND IMMATURE: Brown above with green sheen. White below. Lacks alar, scapular, back patch and caruncle. Upper mandible brown, lower white. Face, legs, and feet pale whitish-pink. Juvenile apparently distinguishable from adult by flaky bill and pointed flight feathers as against rounded tips of adult remiges.

Field characters

Large black and white shag with long, prominently hooked and stout bill, long neck, heavy body, short broad wings and short legs and tail. Within its range can be confused only with pied cormorant which is much whiter on face and neck, lacks white patches on wings and back and has black legs and feet. Flight evocatively described as 'batlike', with head held below body axis. Pied has longer wings and tail and holds neck in an 'S' in flight. King shag appears large-headed and thick-necked in flight. Chatham and pied morph of Stewart resemble king shag (c76 cm) but smaller (Chatham 63 cm, Stewart 65–70 cm) and have own discrete ranges. All 3 species dark-headed with some black on face. All dark on back, white below, and have variably conspicuous white alar and dorsal patches; pinkish legs and feet. Early in breeding all have black forehead crest, scattered white filoplumes on neck. Facial caruncles prominent in king shag, face blue-grey, but in Chatham bright orange and Stewart dark purple-brown (Marchant and Higgins 1990).

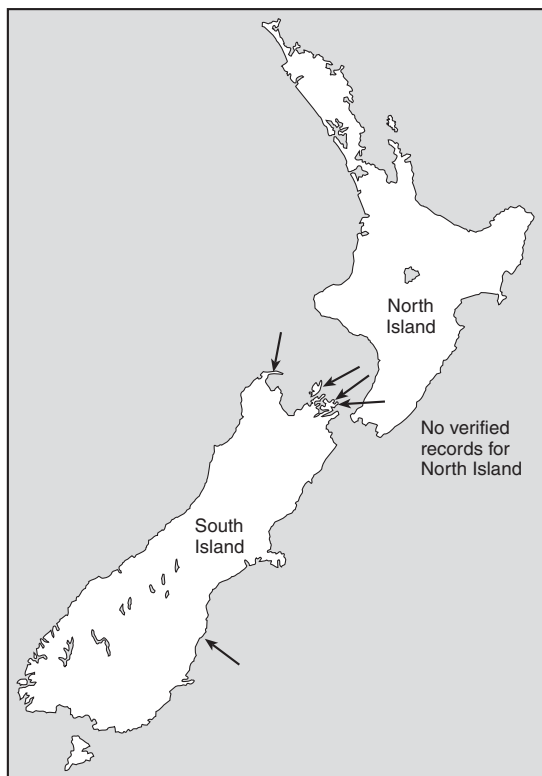
Measurements (see Appendix)

Voice

Few details. Repeated 'ergh-ergh' interpreted as probable male threat.

Range and status

Rare; total population c524 individuals (Schuckard 1994). Endemic to Marlborough Sound area of



6.132 Breeding distribution king shag (*P. carunculatus*). (From Marchant and Higgins 1990.)

New Zealand (NE of South Island). Breeds at Te Kuru Kuru Island, North Trio Island, Duffer's Reef, Sentinel Rock and White Rocks. Persecution by fishermen and disturbance by pleasure boats and skin-divers has endangered this shag; classed as 'threatened' by ICPB. Recovery of fossil bones (late Holocene) N New Zealand indicates present population a relict.

MOVEMENTS: Few recoveries outside breeding areas.

Foraging and food

Forages in small groups or singly. Dives av 46.5 sec (up to 95) (A. Nelson 1971). Sometimes swallows pebbles. Food includes bottom-dwellers; sole *Peltorhamphus*, sand-eels *Gonorhynchus*, blue cod *Paraperis*. Of 683 prey items 90% *Amoglossus scapha*

(pellet analysis, Lalas and Brown 1998). Only 1–3% of diet of interest to commercial or recreational fishermen.

Habitat and breeding biology

(See Fig. at end of ch. 5; A. Nelson 1971)

HABITAT: cold-water cormorant of sheltered inlets and bays, nesting on pinnacles, slopes, and plateaux of rocky islets, sometimes barely 1 m above av HWM; nests sometimes sheltered by scrub.

COLONIES: Small numbers preclude large gatherings but typically breeds in small colonies. Extremely timid and colonies should not be closely approached.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually although two cycles sometimes attempted if breeding begins early in year ($n=6$). Breeds mainly March–Dec, often starting around May and finishing laying by Aug. Complete breeding cycle \approx 5 months.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: During threat raises feathers of hind-neck forming broad ruff. Weaves head back and forth and sideways in irregular, sinusoidal movement with bill somewhat open but not gaping widely. No details concerning overt fighting.

Male sexual advertising involves usual cormorant throwback, taking head in vertical arc until nape touches rump where, although it does not rotate it may 'bounce' a few times before being brought forwards. Bill open or closed. Body horizontal. During typical interaction of partners when meeting on site (so-called 'recognition') birds gape and then lower head and extend neck whilst moving it up and down, bill closed. Often, this display is synchronous. Pre-take-off posture is a forward-upright, bill slightly gaping and bird swallowing. May 'kink-throat' after landing and when approaching nest-site. After landing, head and neck lowered horizontally in exaggerated manner. When walking in vicinity of nest upper neck strongly kinked and bill (closed) inclined forwards. Before hopping, neck strongly arched, bill pointing down. Here, as also preceding take-off, throat pulsates.

COPULATION: (GFA)

NEST: Vegetation and guano. Approx c50 cm across, 40 cm high on downhill side (slope often severe). Cup c27 cm diameter and 7–10 cm deep. Nests usually c. 1 m apart. Male presumed to gather most or all nest-material.

EGG/CLUTCH: 65 (63–67) × 41 (40–3); 68 (62–75) × 43 (42–5) n = 7. Weight 62 g n = 2. Clutch 1–3. No information about replacement laying.

INCUBATION: Shared; period not recorded.

CHICK/BROOD: Down smoky brown. No details of brood.

CARE OF YOUNG: Shared. Few details.

BEHAVIOUR OF YOUNG: No details.

BREEDING SUCCESS AND OTHER ASPECTS OF LIFE CYCLE: Few details but suspected often to use same site in successive breeding attempts; may be significant fidelity to mate.

Stewart Shag *Phalacrocorax chalconatus*

PLATE 9

Graculus chalconatus Gray, 1845, South Island New Zealand.

Referred by Siegel-Causey to *Eleucocarbo*, by Johnsgard to *Leucocarbo*. Considered by some to be one of 3 sub-species of king shag *carunculatus*.

Other common names: Stewart Island shag, Gray's shag, pink-footed shag, bronze shag, Stewart Island cormorant.

French: cormoran de Stewart, cormoran bronze. German: Stewartscharbe. Spanish: cormoran de la Stewart.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Occurs in two morphs, pied and bronze. Pied much resembles king *carunculatus* with same dark-headed look due to black of head extending well below eye to borders of chin. Black continues down hind-neck to join with dark, green-sheened back. White patches on upper wing, scapulars may be prominent, variable or absent. Rump, upper tail coverts, tail and thighs black with blue sheen. Throat, foreneck and remainder of underparts white. Long white filoplumes scattered on head and neck and forehead sports long, black crest. Pink or grey bill has orange-red caruncle at base. Eye-ring iridescent

purple-blue; face and gular skin purplish brown (gular sometimes light red). Eye dark brown. Legs and feet pinkish. Bird with yellow feet recorded at Taiaroa Head. By contrast bronze form entirely dark with blue body sheen and green gloss on wings. Confusingly, a few intermediate birds with mixture of white and black on underparts.

ADULT F: Similar.

POST-NUPTIAL: Plumage remains basically similar but lacks crest and filoplumes and has dull soft parts and blue eye-ring.

JUVENILE AND IMMATURE: Juveniles also dimorphic; but duller than non-breeding adults with dark brown upperparts usually lacking white patches on wing and back; white or dark brown underparts. Bill light coloured, face dark brown with yellow at gape, eye-ring grey, iris brown. Legs and feet flesh. No facial papillae. Mating non-assortative. Otago birds larger, with much larger caruncles than Foveaux Strait ones; could support view that this shag is sub-species of *carunculatus*.

Field characters

Large with long, stout bill, heavy head and body, broad, short wings. Difficult to separate from king *carunculatus*. But Stewart is smaller, has red-orange in gular area, deeper pink feet. Pied morph could

perhaps be confused with pied cormorant, which has more white on face and neck, typical cormorant's longer wings and tail, S-shaped neck in flight and black legs and feet.

Measurements (see Appendix)

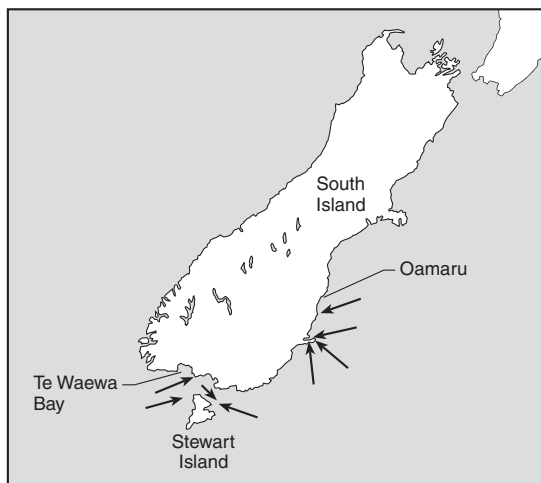
Voice

Barking 'corr-corr-corr'; soft 'eh-eh-eh' (see Auckland shag *colensoi* for probable contexts).

Range and status

Stewart Island and adjoining islands (Codfish and islands in Foveaux Strait) and SE of South Island from Oamaru to Te Waewae Bay, W of Invercargill. Considered to be under threat and 'rare'. Estimated 1,500–2,000 nesting pairs and some 12 known breeding sites: 4 between Dunedin and Otago, 4 Stewart Island, 2 Codfish Island, 1 each Centre Island and Bluff Harbour. Largest known colony on Centre Island, 1955 *c.* 1,200 birds. Picked up on New Zealand (South Island) beaches (Otago and Southland) mainly in summer.

MOVEMENTS: Apparently sedentary.



6.133 Breeding distribution of the Stewart shag (*P. chalconatus*). (From Marchant and Higgins 1990.)

Foraging and food

Feed (usually solitarily?) on or near seabed at depths of 1–30 m, up to 15 km offshore and only during daylight. Apparently search bottom by zig-zagging, flushing concealed prey by probing. Dives vary in duration according to depth of water, 8–169 sec. Diving bouts vary from c2 hr in water 5 m deep to 45 min in water 25 m with rest periods of up to 2 hr between bouts, during which remain on water or come ashore. Rough seas seem not to inhibit feeding but strong winds prevent flying. Birds leave roost at sunrise and return midday–sunset. Food 70% fish supplemented with marine invertebrates, mainly crabs (25%; up to 160 g), octopus (up to 90 g), polychaetes (C. Lallas in Marchant and Higgins 1990, from c28,000 prey items from pellets). Very small fish (*Tripterygion*) comprise 35% by weight of fish prey but on av measure only 4 cm, max 9 cm, and weigh on av only 1 g). Fish most important in spring (85% by weight), least in winter (45%) when crustacea (40%) and cephalopods (15%) assume greater importance. Daily intake c330 g (110–760 g), number of items 180 (5–535). Intake *c.* 11.8% adult weight.

Habitat and breeding biology

(See Fig. at end of ch. 5; Marchant and Higgins 1990)

HABITAT: Marine sedentary shag of inshore waters off rocky coasts and around islands. Nests on headlands or small, rocky islets perhaps with moss and dwarf vegetation of *Mesembryanthemum*.

COLONIES: Apparently 'structured', with experienced pairs occupying higher areas. Immatures (and adult-plumaged non-breeders?) gather nearby.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually. Apparently may lay at almost any time depending on year, location and (presumably) food. Reputedly, a colony may contain all stages from new nests to fledged young.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Much as king shag but during male advertising body said to be upright rather than horizontal though perhaps both species use both positions under different circumstances (my comment). Otherwise

gaping and head-lowering during pair-interactions (so-called recognition) seem same as king shag. Gaping claimed to differ in degree in two species but this remains to be elucidated (respective illustrations in Marchant and Higgins unconvincing). Males 'kink-throat' and call on arrival; females silent.

NEST: Pedestal up to 1.5 m high made of vegetation, humous and guano with grass-lined cup.

EGG/CLUTCH: 63 (59–69) × 41 (41–2) n = 5; 66 (56–70) × 42 (40–4). Calculated weight 48.6 g. Clutch 2–3.

REPLACEMENT LAYING: Presumably occurs.

INCUBATION PERIOD: 28–30 days?

CHICK/BROOD: Black-skinned downy young of pied morph are smoky brown with tufts of white filoplumes. Bronze morph said to be pale to dark

brown with a few white filoplumes on upperparts, rather more on underparts. Down thick and woolly including most of head. Naked gular pouch pinkish-buff. Bare skin on front of crown and part of face grey-black. No information on brood-size but likely to be 2.

FLEDGING: Little useful information on development and behaviour of young or their fledging period and post-fledging feeding, though known to maintain contact with adults. After fledging, young form groups away from centre of colony.

BREEDING SUCCESS: No information.

FIDELITY TO COLONY, SITE, AND MATE: Pair-bond, and therefore site, thought to be maintained over more than one season.

OTHER ASPECTS OF LIFE CYCLE: No information.

Chatham Shag *Phalacrocorax onslowi*

PLATE 9

Phalacrocorax onslowi Forbes, 1893, Chatham Islands.

Sometimes placed in *Leucocarbo* or *Euleucocarbo*. Considered by some to be sub-species of *carunculatus*. Some authors merge not only *carunculatus*, *chalconotus* and *onslowi* but also *campbelli*, *ranfurlyi* and *colensoi* into single species.

Other common names: Chatham Island shag/cormorant.

French: cormoran des Chatham. German: Chathamscharbe. Spanish: cormoran de las Chatham.

Sub-species

Monotypic.

Description

Much as king shag *P. carunculatus* and pied form of Stewart shag.

Field characters

See king shag for comparison with Chatham and Stewart. Restricted distribution of two latter is helpful since (size excepted) under poor conditions separation of 3 species could be impracticable even for experienced observer. Pitt shag also occurs in Chathams but grey beneath, lacks orange caruncles.

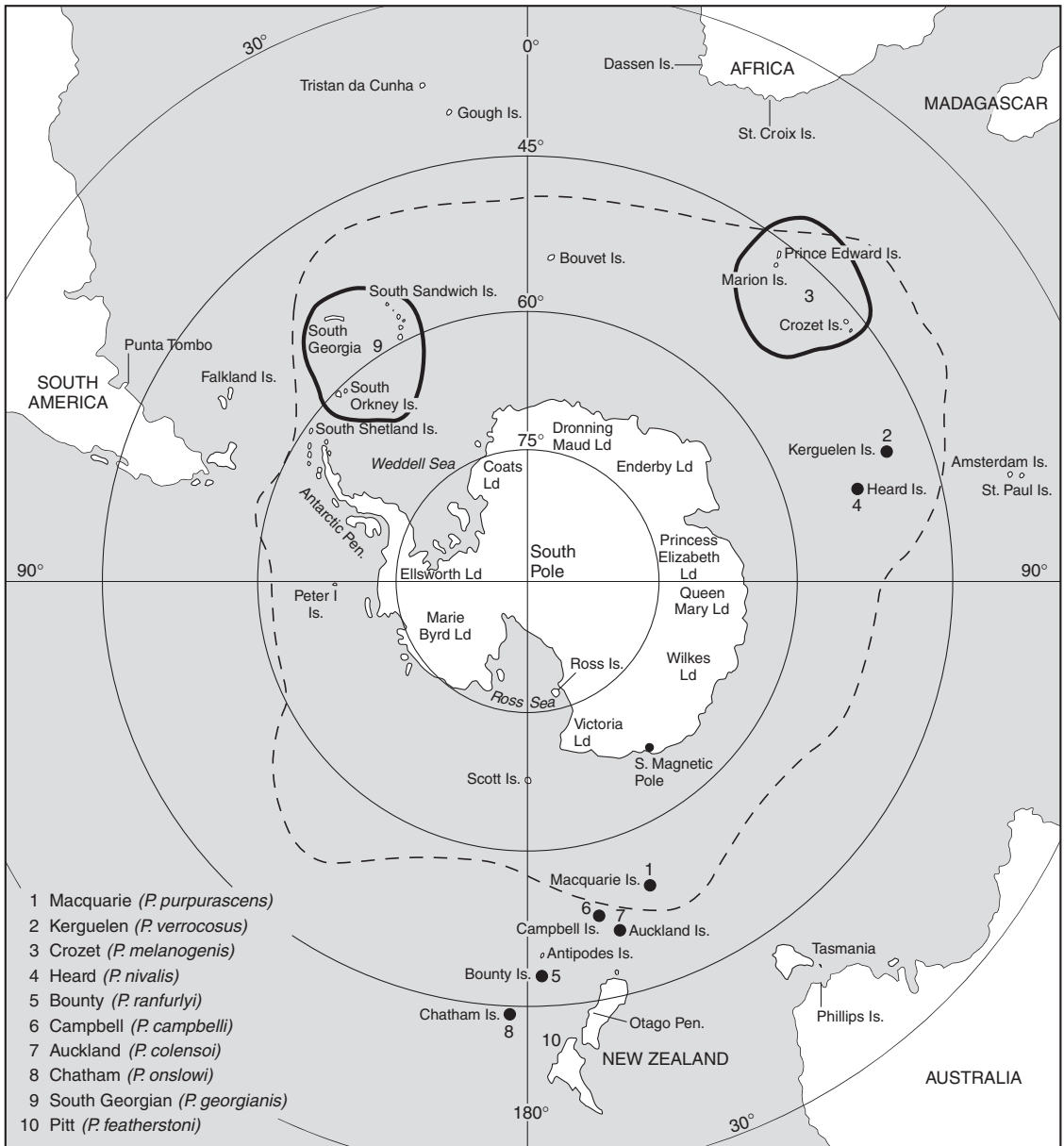
Measurements (see Appendix)

Voice

Male aggressive, loud, 'ergh'. During sexual advertising a loud 'borr' or 'rogh'. A barking 'heh-heh-heh' during gaping display and a pre-departure, pre-hop ticking 't-t-t'. During kink-throat a repetitive 'corr-corr-corr'. Female a soft 'ghff-ghff' during gaping, but largely silent.

Range and status (Figure 6.134)

Chatham Island group, usually within few km of coast. Imber (1994) records for 1961 breeds



6.134 Distribution of shags in the sub-Antarctic and Antarctic zones.

Chatham, Manukau Point, (80 nests), Okawa (c68 nests), Matarakau (c50 nests), Nga-toka Turua (c37 nests), Whangamoe (5 nests), Weeding Point (10 nests). Te Whanga lagoon, Motuhinahina Island (40+ nests, 1986). Manukau Point colony subsequently moved close to Cape Fournier, where vulnerable to disturbance and

colony abandoned by 1988. Sker-Keys Island, 358 nests with eggs or chicks in 1977. Colony c80 nests (1980) on top of Rabbit Island. Species classified as 'threatened'.

MOVEMENTS: Sedentary; not recorded away from Chatham Islands.

Foraging and food

Marine; fairly inshore in bays and inlets and along sheltered shores. Probably similar to close relatives.

Habitat and breeding biology

(See Fig. at end of ch. 5; van Tets in Marchant and Higgins 1990)

HABITAT: Rocks, small islands, and broad cliff-ledges from just above HWM to more than 15 m.

COLONIES: Small groups of up to 50 nests.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually. Eggs laid Sept–Dec but variable between and within colonies.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Very similar to king and Stewart Island shags. Male's sexual advertising performed from standing position with body nearly vertical as head thrown back to rump. Throwback repeated up to 13 times and may be silent or accompanied by loud 'rogh-rogh'. Accordingly, bill may be closed or wide open. Gaping and head-lowering seem identical to

king and Stewart shags (up-and-down head movement depicted for head-lowering in king and Chatham shags but not for Stewart shag, in Marchant and Higgins, probably not to be taken as diagnostic). Similarly, differences (if any) in pre-take-off, pre-hop, post-landing and kink-throating displays between these 3 shags remain to be described.

NEST: Vegetation.

EGG/CLUTCH: 61 (59–63) × 39 (37–40) n = 4; 61 (56–66) × 39 (37–40) n = 8; 61 (58–64) × 40 (34–44) n = 20. Calculated weight 48.6 g. Clutch usually 3; 4 recorded.

INCUBATION PERIOD: Presumably c29 days.

CHICK/BROOD: Downy young similar to king and Stewart shags with smoky brown down and some white filoplumes. No information on broods.

No details on development, fledging period, post-fledging care, breeding success, age first breeding, mortality rates etc. but unlikely to differ much from close relatives.

Auckland Shag *Phalacrocorax colensoi*

PLATE 9

Phalacrocorax colensoi Buller, 1888, Auckland Islands.

Sometimes placed in *Leucocarbo* or *Euleucocarbo*.

Often considered race of *P. campbelli*. Some authors merge *colensoi*, *campbelli* and *ranfurlyi*, together with *carunculatus*, *chalconatus* and *onslowi*.

Other common names: Auckland Island cormorant. French: cormoran des Auckland. German: Auckland-scharbe. Spanish: cormoran de las Auckland.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Similar to others in this closely related group. Neck and throat area variable in that white may be largely restricted to throat and

only narrowly joined to white underparts, most of side neck being black. Long, black, recurved crest, variable alar patches (prominent to absent), occasionally white scapulars. Bill black or dark grey with orange tip to lower mandible. No caruncles at base of bill but long, warty, orange line from base of upper mandible to gape, short line of orange skin at base of lower mandible. Eye ring violet to purple, face purple to red. Gular pouch, mouth lining orangy. Eye dark brown or purplish. Legs, feet pink.

ADULT F: Similar.

POST-NUPTIAL: Loses crest, black fades to brown and face dulls.

JUVENILE AND IMMATURE: Brown, glossed green. Alar patches absent or sandy and may be brown band or spots across foreneck. Facial skin brown.

Field characters

Comparatively small (length c63 cm) and confined to Auckland Islands. Closely resembles Campbell shag but *campbelli* has uniform black on throat and foreneck ending in clean line across base of throat and neck. *Campbelli* is said never to show white feathers on back but illustrations show conspicuous white in alar area though less than in related forms.

Measurements (see Appendix)

Voice

Advertising males utter raucous bark 'orr-orrgh' or 'borr'. During threat repeated 'erh-erh-erh'; pre-take-off 't-t-t' or 'hu-hu-hu' which during hops ends with variable, drawn-out 'owhrr'. During regurgitation of pellets males utter accelerating 'gock-gock-gock'. Females may emit soft 'ff-ff' or 'eh-eh' during gape and threat. Similar sounds emitted during hops and when regurgitating pellets.

Range and status (Figure 6.134)

Restricted to Auckland Islands (where only cormorant) and nearby waters. Breeds on Auckland (<2,000 birds), Enderby, and Cape Crozier.

MOVEMENTS: Sedentary, though may forage well out to sea (50+ km?).

Foraging and food

Solitary or gregarious, inshore or well offshore, where may feed in large flocks, taking fish (e.g. pilchards, Clupeidae), crustacea and probably other items though little information. Food residues and debris regurgitated as wrinkled, pink pellets.

Habitat and breeding biology

(See Fig. at end of ch. 5; van Tets in Marchant and Higgins 1990)

HABITAT: Nests, unmixed with other species, on top of steep cliffs, on ledges, on bare ground, among tussock grass, beneath bushes or trees or often beneath overhangs on cliff-ledges.

Low-lying nests may be destroyed by high tides or storms.

COLONIES: Large or in small groups; nests c75 cm apart, centre to centre.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually? Eggs laid from at least Nov–Feb.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: According to figures in Marchant and Higgins, strongly resembles near relatives. Males advertise from almost vertical position with drooping wings and cocked tail. Throwback repeated many times, slowly and irregularly with closed or open bill. No mention of head rotation but loud barking call may be uttered as head touches rump. 'Gaping' accompanied by raucous barking in male and barely audible puffing sounds in female whilst upper-breast and lower neck pulsate. Nothing distinctive reported about remainder of on-site ritualized behaviour.

NEST: Shallow mound of vegetation such as tussock grass, seaweed, humus, debris and twigs. Maintenance involves re-arranging material; may enhance insulation.

EGG/CLUTCH: 62 (55–66) × 39 (36–49) n = 32. Calculated weight 47 g. Clutch probably usually 3, laid at intervals of 48–96 hours.

INCUBATION PERIOD: Egg 1 28–32 days; egg 2 26 days.

CHICK/BROOD: Hatches with grey or black skin, becoming clothed in grey down. Throat and lower mandible pink. Brood usually 2. No details of development, behaviour, fledging period etc.

BREEDING SUCCESS AND OTHER ASPECTS OF LIFE CYCLE: Few details. Skuas significant threat to eggs and young.

FIDELITY TO SITE: thought to be fairly strong unless cover is lost, whereupon site vacated.

Campbell Shag *Phalacrocorax campbelli*

PLATE 9

Urile campbelli Filhol, 1878, Campbell Island.

Sometimes placed in *Leucocarbo* or *Eleucocarbo*. Together with *P. colensoi* and *P. ranfurlyi* sometimes considered conspecific with *P. carunculatus* complex (*carunculatus*, *chalconatus*, and *onslowi*) (Voisin 1973).

Other common names: Campbell cormorant. French: cormoran de Campbell. German: Campbell-scharbe. Spanish: cormoran de la Campbell.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Unlike close relatives front and sides of neck black, as well as head and hind-neck. Small white patch on chin and throat and sharp demarcation between lower border of black foreneck and white breast, underparts. Conspicuous contrast between white and black on side neck, characteristic of its congeners, here missing. Long, black, recurved crest on forehead; long white filoplumes scattered on sides of head. Back dark with green sheen; indistinct black borders to feathers. White alar patch variably developed, no white on scapulars or back. Wings (including underwing), tail, thighs blackish. Bill dark orange-brown or grey-brown, lacking caruncles but with orange line above gape, orange spot at base of lower mandible. Eye-ring, face purplish, gular pouch reddish, eye dark browns. Legs, feet pink with dark blotches.

ADULT F: Similar.

POST-NUPTIAL: No crest or head plumes; gape-line and spot yellow.

JUVENILE AND IMMATURE: Dark brown where adult blackish; lacks alar bar; bill light orange-brown, yellower at base; face dull purple, gular pouch dull yellow-orange. Eye brown-grey. Legs, feet dull orange, pink and grey.

Field characters

Closely resembles Auckland and Bounty shags but ranges do not overlap. Black foreneck and sharp demarcation between lower foreneck and white upper breast characterizes Campbell shag.

Measurements (see Appendix)**Voice**

Males bark 'korr-korr' during some displays but scant information.

Range and status (Figure 6.134)

Restricted to Campbell Island though possibly some vagrancy. Population, 1975, *c.* 2,000 nests and (guessed) total population *c.* 8,000 birds (Marchant and Higgins 1990). Not considered endangered.

MOVEMENTS: Probably almost entirely sedentary though vagrants of this species (or Bounty shag) have reached Antipodes (800 km).

Foraging and food

Marine inshore to far offshore. May forage in flocks of 20–2,000, sometimes tight but then forming lines, dipping heads into sea and beating water with wings before diving singly or in groups until most, or all, submerged. Large foraging flocks may dive entirely synchronously. Usually 'jump-dives' and may swim long distances underwater before surfacing and dispersing or swimming back into formation and repeating process. Feeding flocks attract petrels, gulls, and terns or may be attracted by them. Feeding habits suggest they are pursuing shoals of fish. Little information on food. One old record of stomachs filled with small molluscs.

Habitat and breeding biology

(See Fig. at end of ch. 5; Marchant and Higgins 1990)

HABITAT: Precipitous cliffs, on narrow ledges, in alcoves or in caves, 12–30 m above sea. Also on

ground among tussocks and on rocky islets. May form loose associations with silver gulls and Antarctic terns, which mob predatory skuas; may protect shags from egg-loss, since skuas attack, displace them and eat their eggs.

COLONIES: Fairly dense and up to 200 nests, though sometimes breeds solitarily.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually? Circumstantial evidence indicates eggs laid Aug–Dec, perhaps mainly Aug–Sept.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Sexual advertising by male apparently silent and performed from sitting position. Throwback lacks rotation of head but head may ‘bounce’ several times on rump or may move laterally. Tail may be cocked up or forwards or held down. Wings droop, crest flattens, and bill gapes

slightly or widely. In ‘gaping’, movement of head complex, not merely back-and-forth but also one to side. During mutual head-lowering throat bulges, emphasizing reddish gular pouch, and participants may stand side by side or facing. Displacement nest-worrying frequent during pair-interactions. Any consistent differences in amplitude of various postures associated with pre-hop, post-landing and similar contexts, between this and close relatives, remain undescribed.

NEST: Flattened heap of vegetation with shallow cup.

EGG/CLUTCH: 67×39 ; 62×39 . Calculated weight c48 g. Clutch presumably 2 or 3.

CHICK: Hatchling black skinned with pink throat becoming covered in grey down.

BREEDING SUCCESS AND OTHER ASPECTS OF LIFE CYCLE: No information.

Bounty Shag *Phalacrocorax ranfurlyi*

PLATE 9

Phalacrocorax ranfurlyi Ogilvie-Grant, 1901, Bounty Islands.

Sometimes placed in *Leucocarbo* or *Eleucocarbo*. Often considered race of *carunculatus* complex.

Other common names: Bounty Island cormorant. French: cormoran des Bounty. German: Bountyscharbe. Spanish: cormoran de las Bounty.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Head, hind-neck black but entire chin, throat, foreneck, underparts white. Back black (blue sheen) but scapulars and mantle dark brown with green sheen and narrow, indistinct black borders to feathers. White alar patch prominent on most but poor on

some. Lacks white scapular patch, though some males have small white dorsal patch. Remainder of upper parts, thigh, tail black. Black underwing has white line (sometimes two) along upper arm. Brown or pink bill with dark culmen and pale tip lacks caruncles at base, which is variable orange-yellow. Facial skin, eye-ring, gular pouch fairly uniform orange to red, forming useful identification feature. Eye light brown. Legs, feet pink with dark blotches.

ADULT F: Similar.

POST-NUPTIAL: Loses crest, colours dull, bill light grey-brown.

JUVENILE AND IMMATURE: Brown above, white below; blackish on wings, back, tail, lacking white alar patches; brown spots or band across foreneck. Bill, face brown; gular pouch grey. Feet pinkish brown.

Field characters

No other shags on Bounty Islands. Most closely resembles Auckland but bigger, less black on fore-neck; redder, more extensive facial skin. No caruncles or blue eye-ring.

Measurements (see Appendix)

Voice

Males utter soft 'borr-borr-borr' during threat; 'he-he-he' during gaping, a ticking 't-t-t' during pre-take-off, a soft 'herr-herr' or 'corr-corr' during kink-throating. Female largely silent.

Range and status (Figure 6.134)

Restricted to Bounty Islands though possibly wanders. In 1978 c. 1,142 pairs on 11 islands. Population sufficiently small and vulnerable to warrant 'endangered'.

MOVEMENTS: Sedentary but see Campbell shag.

Foraging and food

(Robertson and van Tets 1982)

Coastal marine. May feed in groups up to 300; no evidence cooperative feeding. Adults and immatures feed in same group. Leap-dives. Contents of 9 stomachs mainly fish but also molluscs, cephalopods, isopods, crustacea and echinoderms.

Habitat and breeding biology

(See Fig. at end of ch. 5; Robertson and Bell 1984; Robertson 1988; van Tets in Marchant and Higgins 1990)

HABITAT: Nests on bare, rocky islands using ledges and alcoves on sheltered faces, or on narrow ridges. May have to compete with penguins and/or albatrosses.

COLONIES: 22–330 pairs (Robertson and Van Tets 1982). Nests densely; c. 1 m between adjacent nests (centres).

FREQUENCY, TIMING, AND DURATION OF BREEDING: Known to lay Oct–Nov.

TERRITORIAL, PAIR-FORMATION AND MAINTENANCE: During threat makes sinuous head and neck movements with gaping bill and (male only) calling. Males advertise from standing position with body becoming almost vertical as head swings back until nape touches rump. Tail cocked and wings drooped. Open bill may snap shut as head returns. Gaping, head-lowering (mates often synchronize) and usual gamut of pre-and-post-landing, pre-hop, kink-throating and ritualized walking.

NEST: c35 cm diameter, 15 cm high, of brown seaweed and debris. Males dive at least 10 m to gather seaweed in surging water which may help to loosen weed. Building, mainly by female, continues during incubation and chick-rearing, when females, too, may gather material.

EGG/CLUTCH: 64 (58–69) × 41 (39–46) n = 20. Calculated weight 59 g. Clutch 2–3.

BEHAVIOUR OF YOUNG AND FLEDGING: No details. No information on remainder of breeding ecology.

Pitt Shag *Phalacrocorax featherstoni*

PLATE 9

Phalacrocorax featherstoni Buller, 1873, Chatham Islands.

Called *Leucocarbo (punctatus) featherstoni* by Johnsgard (1993) but *Stictocarbo featherstoni* by Siegel-Causey (1988), who thus, along with Marchant and Higgins (1990) and Sibley and Monroe (1990) give it species rank.

Other common names: Chatham Islands shag, double-crested cormorant (sic!). French: cormoran de Featherston. German: Pittscharbe. Spanish: cormoran de la Pitt.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: A smart shag resembling spotted shag but lacking white stripe down side-neck. Head, throat, neck blue-black, as is lower back and rump. Mantle, scapulars, upper wing-coverts dark, green-glossed olive brown, each feather with black terminal spot. Black tail feathers have shafts grey at base. Lower foreneck, breast, upper abdomen smooth, pale grey terminating in black lower abdomen and under-tail coverts. Forehead sports prominent, recurved crest; second crest, also curling up at ends, on nape. Dense white filoplumes hindneck; scattered ones elsewhere on head and neck. Bill long, slender, blackish with light brown tip; small creamy patch at base of lower mandible. Face grass green, gular skin black with blue-green warts. Eye red-brown. Legs, feet yellow-orange.

ADULT F: Similar.

POST-NUPTIAL: Loses white plumes and crests, gular skin becomes greenish instead of adorned-black.

JUVENILE AND IMMATURE: Juvenile brown with greenish tinge on head, neck, back, wings, tail but not uniform. Numerous filoplumes on head and neck. Darker tips to back feathers impart somewhat spotted appearance. Breast and upper abdomen pale; throat, foreneck and sides of neck paler than hindneck. Thighs and under-tail-coverts dark with bluish tinge. Bill light coloured, face and eye-ring pale yellowish; eye brown. Legs and feet pale yellow.

Field characters

Small, slender, marine shag with sinuous neck, slender wings, short tail. Found only around Chatham Islands. Unlikely to be confused with other species; only one with black spots on grey upperparts. Campbell has white underparts and pink feet.

Measurements (see Appendix)

Voice

Gargling 'argh-argh-argh' associated with threat. Pre-departure 'ticking' running into blurred 't-t-t-t' during hop. An 'oh' sound follows landing.

Range and status (Figure 6.134)

Endemic to Chatham Islands (Chatham, Pitt, Big and Little Sisters, Mangere, Little Mangere, Rabbit Island, The Castle). Total population probably fewer than 1,000 birds but not thought to be endangered.

MOVEMENTS: Sedentary.

Foraging and food

Often forages among kelp and in groups of adults and juveniles around coasts and rocky islands, although thought to feed well offshore at times.

Habitat and breeding biology

(See Fig. at end of ch. 5; Marchant and Higgins 1990)

HABITAT: Cliff-ledges and in niches and crevices of steep faces.

COLONIES: Breeds in groups, less colonial than Chatham shag. Spacing probably largely dictated by topography.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually. Laying said to begin Aug and post-fledging feeding of young completed by early Feb.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Male selects site; behaviour closely resembles spotted shag. Male sexual advertising consists of wing-flicking at *c.* 4 times per sec with head in typical backward position followed by swinging head and extended neck forwards and backwards in an upwardly directed arc 'swing-pointing' but never laying head right back onto tail, nor rotating it. Also, either sex may 'bow', taking bill to ground or nest, with forwardly arched neck. 'Darting', in which with upwardly pointing bill bird retracts and extends its neck, is performed as 'recognition' display by 'in' bird (doubtless homologous with darting, part of sexual advertising in some shags). An elongated posture, either upright or horizontal, with kink-throat and pulsations at base of throat, commences by raising body from horizontal position adopted when darting. This behaviour, also, said to be used as

recognition. In this shag, apparently, recognition does not involve gaping, even though it does in behaviourally similar spotted shag (but see below). Other displays used on or near site: pre-take-off posture, not much different from upright position but bill horizontal or pointing down and throat bulging, rather than base of neck pulsating, and feathers at base of neck and on nape raised. Males may 'tick' softly; females silent. After landing, and probably during inflying, birds 'kink-throat' with head flattened laterally 'discoidal' and bill gaping. This passes into a post-landing posture with closed bill above horizontal and neck feathers ruffed. Males call but females silent. Apparently this shag lacks spotted shag's pre-hop posture (arched neck and downward-pointing bill).

As yet, observations on shag behaviour have been too cursory to be dogmatic about details

such as bill position, tail position, angle at which neck held, degree to which various feather tracts raised or throat bulged, in several displays which may feature these subtle 'qualifiers'. Would be unwise to read too much into their supposed functions or into supposed differences between species.

NEST: Small; various plant material. Refurbishes old nests. Female builds with material brought by male.

EGG/CLUTCH: 58.1 (55.2–61.4) × 34.8 (32.5–36.8) n = 8; 58.0 (56–61) × 35 (33–8) n = 10. Calculated weight 39.2 g. Clutch usually 3.

No details on breeding success and other aspects of life cycle.

Imperial Shag *Phalacrocorax atriceps*

PLATE 8

Phalacrocorax atriceps King, 1828, Strait of Magellan

Other common names: imperial blue-eyed shag (see introduction to group), blue-eyed shag or cormorant, Antarctic blue-eyed shag, Antarctic shag, emperor shag, rock shag, king shag, Falkland blue-eyed shag, crested shag, Magellanic blue-eyed shag and common names of species given under SUBSPECIES. This group is a nomenclatural jungle.

French: cormoran impérial. German: blaueaugenscharbe. Spanish: cormoran imperial, guanero.

Sub-species

Race *albiventer* formerly considered to be separate species comprising birds from Falkland Islands and parts of South America but wide zone where mixed pairs of *atriceps/albiventer* occur (Siegel-Causey 1986a). Also these two inseparable on osteological characters or behaviour. Thus *albiventer* constitutes only race or maybe colour morph of *atriceps* and is so considered here. Some authors include *P. melanogenis*, *P. verrucosus* and *P. purpurascens* with supposed *P. albiventer*. *P. atriceps* has also frequently been considered to include *P. bransfieldensis*, *P. georgianus* and *P. nivalis*. All above forms

sometimes now placed in genus *Notocarbo* rather than *Phalacrocorax*.

Description

ADULT M PRE-BREEDING: Crown, nape, hind-neck blue-black; ragged crest. Line of demarcation between white cheeks and dark crown about level with eye. Lower cheeks, chin, foreneck, underparts white, upperparts blue-black with median white dorsal patch mid-back, white alar patches. Wings, tail black. Eye brown to pale green, eye-ring bright blue, nasal caruncles yellow though variable in shade and shape, with orange marks between eye and gape. Facial and gular skin dark speckled with yellow, bill greyish or olive with horn-coloured tip to lower mandible. Legs, feet pinkish.

ADULT F: Similar.

POST-NUPTIAL: Lacks crest, caruncles shrink and coloured parts become dull. White alar and dorsal patches may be smaller or absent and do not reappear until some time after crest has regrown.

JUVENILE AND IMMATURE: Lacks crest and, usually, alar patches, though if present these are mottled pale brown. Wings, lower back browner, edged grey/white and more pointed. Crown, hind-neck black grading into browner on cheeks. Chin, throat, foreneck white, maybe streaked brown. Eye brown, eye-ring purplish-brown. Bill dark, gular skin bluish. Legs, feet grey. Immature intermediate between juvenile and definitive plumages; some gloss on back but wings remaining brown; head lacks crest; breast may be streaked. White dorsal patch may appear after 2nd summer. Eye brown, eye-ring dull blue, facial skin and caruncles purplish. Legs, feet turning pink.

Field characters

Unreliably distinguishable from birds many call king shag *P. albiventer*; patterns of cheek and dorsal area only external differences. In most cases (see Devillers and Terschuren 1978) line dividing dark from light plumage on head is high in *atriceps*, lower and cutting across cheek in *albiventer*. Thus head of *albiventer* appears almost black whilst that of *atriceps* seems mostly white. They note that this is distinctive and even creates optical illusion of different silhouettes. And only *atriceps* acquires squarish patch of white feathers on back after breeding season.

Measurements (see Appendix)

Voice

Little known. Probably largely silent away from breeding-site, at which males may utter barking 'aark' during aggressive encounters. Females may hiss.



6.135 Imperial shag, Falkland Islands. (Photo: A.K. Kepler.)

Range and status (Figure 6.136)

Breeds coastal South America from Cape Horn and Tierra del Fuego N to Mocha Island, Chile and Punta Tombo, Argentina (where overlaps with guanay cormorants). Chubut, Argentina, c30,000 adults breeding in 1980s (Punta 1989). On Patagonian coast (Argentina) relatively abundant and widely distributed, overlapping with red-legged (Yorio *et al.* 1999). Breeds Lago Vinter (Argentina). Occurs on lakes in Andean foothills up to 800 m (del Hoyo *et al.* 1992). Good numbers in Chile and on lakes of Tierra del Fuego—e.g. Lago Nahuel Huapi (protected area). Common on Falklands (separated by some as *P. albiventer*). At least occasionally breeds King George (S Shetlands) (Hahn *et al.* 1998). Subject to mass mortality on occasion.

MOVEMENTS: No proof that moves far from breeding areas. Immatures may be 80 km out to sea.

Foraging and food

(See Antarctic shag, sometimes treated synonymously.)

May forage offshore in dense masses or solitarily. Mainly bottom feeder at depths up to 50 m often above kelp, in which context feeding alone or in small, scattered groups might be expected to be norm. Kato *et al.* (1999) found that although both sexes spend equal amount of time submerged per day, males (15–20% larger) dived deeper and longer. Food mainly fish supplemented by benthic invertebrates (see Johnsgard 1993 for summary). At Nahuel Huapi main prey freshwater crustaceans (*Sammastacus spinifrons*, *Aegala abtao*) (Rasmussen *et al.* 1993). At Punta Loberia (Argentina) 11 teleost fish species and various invertebrates identified. *Tripterygion cuninghami* most frequently occurring; up to 70 in one stomach. Next commonest anchovy (*Engraulis anchoita*) and *Raneya brasiliensis* (Gosztonyi and Kuba 1998).

Habitat and breeding biology

(See Fig. at end of ch. 5; Siegel-Causey 1986a, 1986b; Johnsgard 1993)

HABITAT: A cold-water marine shag of rocky coasts, often highly gregarious, packing rocks of



6.136 Distribution of the imperial (emperor) shag (*Phalacrocorax atriceps*) including the Falkland Island population which some authors treat as the race (or population) 'albiventer' of the species *atriceps* whilst others call it a full species and yet others part of a superspecies [*atriceps*].

labyrinthine coast of southern tip of South America with 'incredible hordes'. Breeds on cliffs, promontories, rocky islets, stacks, and among tussocks. On cliff-ledges nests may be arranged in rows beneath

overhangs where softer rock has eroded away. Many choose windward sides of islands although they feed in more sheltered waters. Murphy (1936), writing about *P. albiventer* in Falklands, says they nest

indiscriminately among rockhopper penguins and black-browed albatrosses, or form huge, 'pure' colonies on terraced rock or among tussock. Sometimes occupy deep and gloomy caves up to 50 m from entrance.

COLONIES: Often contain thousands of pairs. On Santa Magdalena in Straits of Magellan early reference to birds 'congregated in their nests literally in thousands, forming a dense, black mass covering many yards . . . Their nests . . . ranged in almost mathematical series, exactly a foot of space intervening between each nest' (Cunningham, 1871). Devillers and Terschuren (1978) found *atriceps* and *albiventer* indiscriminately mixed in proportion 80:20 on Isla Chata (5,000–10,000 nests).

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually, in spring. Peak egg-laying season varies with locality from about June–Jan becoming progressively later at higher latitudes. On Deseada (Argentina) arrive early August,

begin laying late October, peak first half November (Arrighi and Navarro 1998). Even within a colony may be wide scatter of laying dates giving rise to mix of eggs and chicks up to well-grown stage. All juveniles and most adults left Deseada in late March.

Although Bernstein and Maxson (1982) refer their account to *P. atriceps*, it is actually a description of Antarctic shag on Anvers Island, here treated as *P. bransfieldensis* (q.v.). At two locations in Argentina Siegel-Causey (1986a, 1986b) studied imperial shag *P. atriceps* and king shag (so-called *P. albiventer* not recognized as a species in this book) in order to compare their courtship with regard to taxonomic implications. Frequently, both these 'species' breed within same colony. Devillers and Terschuren (1978), though on inconclusive evidence, concluded that 15–20% of members of sympatric populations of these two 'species' in Argentina were intermediate in plumage, that mixed pairs did exist and that king shag *albiventer* should at best be considered a sub-species of imperial shag.



6.137 Colony of imperial shags, Bleaker Island, Falklands. (Photo: A.K. Kepler.)

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: During aggressive territorial behaviour or threat, site-defenders gape and 'snake-neck', a sinusoidal waving of extended neck, sometimes with rapid forward thrust and withdrawal repeated several times. This behaviour seemed identical in 2 'species'. During male advertising, at full throwback, movement identical in both *atriceps* and so-called *albiventer*, and in most cases involved single rotation of head in throwback position. Hint that *albiventer* tended to head-roll more often than did *atriceps*. During on-site pair-interactions partners 'throat-clicked' (no sex-difference) standing side by side with head and neck lowered and extended and cheeks almost touching. Before and after copulation partners faced each other and female nibbled or grasped tip of male's bill and moved her head from side to side with gaping bill. Male might remain motionless, preen female or head wave. Amongst commonest pair-interactions, usually referred to as recognition displays (though occurring, also, in lone birds) were 'pointing'—a forward stretch with closed bill and neck feathers erected—and 'darting'—retracting head until it lay over the back and then moving it rapidly from side to side 2–5 times (readily recognizable as homologue of head rotation in sexual advertising of some other cormorants). Sometimes pointing combined with darting (usually male). Males displaying alone tended to preen (mainly alar bar) immediately afterwards. Association of threat with sexually motivated 'advertising' is common; odd that Bernstein and Maxson never observed pointing and darting, or indeed nest-touching, in Antarctic shag.

Imperial shags perform ritualized hop with downward-pointing bill and ritualized walk. Before landing, and in several other contexts, they depress hyoid (kink-throating) accompanied by slight lateral head-waving. This display reveals yellow gular pouch and is frequent when approaching nest, landing near other cormorants or even landing alone.

Siegel-Causey could not detect any difference between imperial-cum-king shags (*P. atriceps* and *P. albiventer* in the terminology of that particular paper) in any of these displays but several apparent differences between these two and Antarctic shags *bransfieldensis*, though this may have been due to incomplete observation of latter.

NEST: Low pedestal or mound of vegetation, humus, debris, and guano with a shallow cup.

EGG/CLUTCH: Falkland Islands 63.1×35.1 $n = 14$. Calculated weight c54 g. Clutch 1–3, usually 3 (Murphy 1936). In Argentina av clutch size over 2 years 2.45 $n = 199$. 60% held 3 eggs (Malacalza 1984).

REPLACEMENT LAYING: Clutches same av size as originals.

INCUBATION: 28–9 days $n = 6$ Argentina. Laying intervals between successive eggs 2 or 3 days; hatching intervals slightly less.

CHICK/BROOD: Hatchling c40 g, initially livid. Turns black, with bluish gular area and bill. Blackish down (browner in some populations) appears after about a week and becomes thick. By end of 3rd week chicks can regulate own body temperature. White down erupts on head, throat, and belly at about time wing and tail feathers begin to emerge. For further details of development, which probably apply to this species, see South Georgian shag *P. georgianus*. Brood-size, Deseada, mid-Dec, 1–4 chicks. By mid-Feb ratio of juveniles (c. 2 months) to adults 1:3.

BEHAVIOUR OF YOUNG: No details.

FLEDGING: Period 75–80 days.

POST-FLEDGING: No details.

BREEDING SUCCESS: (Deseada) Hatched from laid: 53%. Fledged from hatched: 60%. Fledged from laid: substantial differences between years and localities, mainly related to availability of food. Breeding success can thus, on these figures, be almost as low as least successful of tropical pelecaniforms, which seems surprising. As with close relatives, kelp gulls, sheathbills, and particularly skuas take eggs and small chicks. Skuas have been suggested to rank alongside starvation as major cause of mortality in some blue-eyed shags and this may apply here.

OTHER ASPECTS OF LIFE CYCLE: See related species.

Antarctic Shag *Phalacrocorax bransfieldensis*

PLATE 8

P. atriceps bransfieldensis Murphy, 1936, South Shetlands.

Often considered race of imperial shag, *P. atriceps* (thus *P. a. bransfieldensis*). Geographically discrete shags of South Georgia region also frequently placed in *atriceps* or in present species but Marchant and Higgins separate them as *P. georgianus*. Antarctic (as also imperial) shag sometimes placed in genus *Notocarbo*, as *N. bransfieldensis*.

Other common names: blue-eyed shag, Antarctic blue-eyed shag, imperial blue-eyed shag.

French: cormoran antarctique. German: Antarktischarbe. Spanish: cormoran Antartico.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Head, hind-neck blue-black with wispy, recurved black crest towards back of head. Lower cheeks, ear-coverts, throat, fore-neck white. Demarcation line between cap and cheeks curves across cheek leaving ear-coverts white. Upper-parts mainly blue-black with conspicuous white alar bar; white patch on back. Tail black. Underparts white except for black thighs. Bill grey-black with pale tip. Facial caruncles bright orange; gular skin black; eye brown with bright blue eye-ring. Legs, feet pink with dark blotches along toes.

ADULT F: Similar.

POST-NUPTIAL: Crest absent, dorsal plumage and soft parts dull and faded, caruncles yellow.

JUVENILE AND IMMATURE: As non-breeding adult but dull brown above; lacking caruncles.

Field characters

Much larger than other blue-eyed shags of sub-Antarctic except for Heard shag *P. nivalis* and has

more white on face. Prominent white alar and dorsal patches; prominent blue eye-ring. Reputed to have larger caruncles than others though hard to judge.

Measurements (see Appendix)**Voice**

Sexes differ; males utter 'aark' call during threat whilst females may hiss. During display only male calls.

Range and status (Figure 6.134)

Antarctic peninsula, c. 10,000 pairs in 56 colonies on coastal islands of Antarctic peninsula; 700 pairs in 21 colonies in South Shetlands; c200 pairs on Elephant Island. Penguins apart, said to be most numerous bird around Antarctic peninsula (Marchant and Higgins 1990).

MOVEMENTS: Birds from Antarctic peninsula may move N in winter to more open water (Marchant and Higgins 1990). Sedentary in part of range.

Foraging and food

Extends farthest S along milder W coast of peninsula, remaining close to land or pack-ice in winter. Foraging skeins fly in long lines or Vs low over water; like closely related species with head held below body axis. In summer forages singly (probably most typical method) or in small, inshore group, but in winter feeds communally often further offshore (Furse 1987). If harassed by skuas will land on water, dive or retaliate. Where pack-ice prevents this, piracy more successful. In non-breeding season returns from foraging in evening. May dive in unison but nature of cooperation, if any, obscure. Primarily bottom feeder; can dive to more than 100 m. Favero *et al.* (1998) cite *Notothenia coriiceps* most important by mass (49%) whereas *Harpagifer antarcticus* most important by number (58%). At Half Moon, South Shetlands, fish comprised 91%

prey items, almost wholly 5 species; *Nototheniops nudifrons* (most frequent), *Notothenia coriiceps* (greatest mass), *Harpagifer antarcticus*, *Trematomus newnesi*, *Gobionotothen gibberifrons* (Barrera-Oro and Casaux 1996). Analysis of pellets and stomachs, South Shetlands showed fish main prey followed by octopods, polychaetes and gastropods (Casaux *et al.* 1997a); they suggest daily intake of adult 1325 g. Relative importance of fish species differed at Nelson Island (South Shetlands). There *Notothenia coriiceps* 58% by frequency, 65% by weight, but *Nototheniops nudifrons* most important by numbers (47%)—all via stomach contents. Octopods, polychaetes and gammarids also taken (Coria *et al.* 1995). Also at Nelson, Casaux and Barrera-Oro (1993) report benthic octopods as the second most important group after fish, though latter represented 90% by weight of total prey. Polychaetes, and pebbles up to a cm diameter, presumed ballast, have been found in this shag's stomach.

Habitat and breeding biology

(See Fig. at end of ch. 5; Bernstein and Maxson 1982; Extensive detail in Johnsgard 1993, under *Leucocarbo atriceps* lumps data from *bransfieldensis*, *georgianus*, *melanogenis*, *verrucosus*, *nivalis* and *purpurascens*)

HABITAT: Bare slopes, N facing preferred because of earlier thaw, and on rocky islets, at high density, or on low, terraced cliffs at lower density. Also nests among tussocks on cliff-edges. Some nests washed away in rough weather. Nests may be built on snow and ice. Often associates with chinstrap and gentoo penguins.

COLONIES: Vary from handful of pairs, often 20–40, up to 800, but any colony can vary between years. Within a colony, marked subgroups where nests can be very close together—sometimes only half-a-metre apart on steep slopes.



6.138 Colony of Antarctic shags, Paulet Island. (Photo: A.K. Kepler.)

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually. Returns to colony mid-July although wears nuptial plumage from about mid-May and courtship apparently not evident until early Sep. Eggs not laid until late Oct. Thus 6 months between assumption of breeding plumage and production of clutch. Why this period should be unusually long seems obscure. Laying occurs over 5–6 weeks, starting about a month after nest-building begins.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: During fighting (rare) grips and jerks opponent's neck or wing. In threat (both sexes) head enlarged by erection of feathers and expansion of gular area and thrust at opponent and waved slowly from side to side, snakelike, whilst exposing orange mouth by gaping. Fanned and partly opened wings further enhance size. Male calls 'a-aark' and female hisses. At highest intensity bird may repeatedly dart gaping bill in rapid back-and-forth head movement. In some shags similar movement associated with sexual advertising (see *atriceps*). Bernstein and Maxson (1982) did not record nest-touching or worrying during threat but noteworthy if this absent.

Even though breeding within colony as whole usually(?) a-synchronous, courtship within nesting group may occur synchronously. Male advertising noteworthy because wing-flicking movement common to many cormorants here vestigial, occurring as just slight movement in some individuals. Throwback, however, well developed and accompanied by 'a-aark' call. Starting usually from squatting position, head is swung back through vertical arc with gaping bill until nape and crown touch rump. As head swings back bird stands, raises its breast and droops its wings. At highest intensity tail cocked towards head, way beyond vertical.

The 'in' bird responds to arrival of partner with typical cormorant slow and sinuous forward movement of head and neck, bill agape. Partners slowly reach over each other's neck, back and forth, first in one direction then at 180°; often extended necks parallel. Whilst most prominent



6.139 Mutual allo-preening in Antarctic shag. (Photo: A.K. Kepler.)

during courtship, it occurs throughout year when partners together on nest and seems more highly ritualized than equivalent in many other cormorant species. In further pair-bonding display partners move heads rapidly back and forth horizontally whilst throat-clicking with gaping bill. This interesting display, possibly related to some others within order, especially within Sulidae, is performed before, during and after copulation and on arrival at nest. Mutual allo-preening occurs.

Like other shags this species shows ritualized pre-take-off, pre-and post-landing behaviour and a ritualized hop. As Snow first noted for European shag, departure from nest or colony has potential for alarming mate or neighbour and perhaps for this reason it is 'signalled' by adopting an elongated upright position, bill lifted. Before landing bird 'kink-throats'. After landing, assumes horizontal, forward-stretching posture with slight lateral head-waving. Ritualized hop slow with downward-pointing bill. Exaggerated 'penguin' walk described as rapid and high-stepping with head held back, bill pressed to neck. It is used during movement through colony, presumably as appeasement.

Particularly when approaching nest but also in many other contexts such as courtship, pre-departure and pair-interactions, 'kink-throat' is used as

'interpolative' behaviour rather than single-function display.

Based on time budgets and physiological data, reckoned that energy expended by male during courtship equals or exceeds that invested in eggs by female.

COPULATION: (GFA)

NEST: Flattened pedestal of regular shape, or a truncated cone, hollow at the top to form a cup. Cemented with excreta. Height c20–5 cm, c40 cm diameter at rim. May be mostly of seaweed, collected by male from seabed, but also of grass, moss, lichen, and detritus including feathers. Both partners build; nest guarded continuously before egg-laying, presumably against pilfering.

EGG/CLUTCH: 64.25 (60–68.5) × 41.4 (39–42.5) n = 4 (Antarctic peninsula). Weight 59.1 n = 13 Anvers Island; 54.7 n = 636 (3-egg clutches). Clutch av 2.5 n = 811 Anvers Island. Laid at intervals of 2.59 days for 3-egg clutches but longer in 2-egg clutches.

REPLACEMENT LAYING: No details.

INCUBATION: Shared, but males more than females; neither spends much off-duty time at nest. Bernstein (personal communication) discovered strong daily rhythms. Females leave colony shortly after sunrise, return early afternoon. Thus males tend to do morning shift (22.00–12.00 hr), females afternoon. Incubation period c29 days.

CHICK/BROOD: Hatchling livid; turns black with bluish gular area and bill. Within 7 days grows brownish-black down; by 18 days well covered and begins to regulate own body temperature. White down erupts on head, throat, and belly at about time flight and tail feathers appear. No information about brood.

CARE OF YOUNG: Small young require protection from skuas, sheathbills, and gulls. Brooded 13–24

days, guarded until 25–40 days. At first males spend more time brooding and less foraging than they did before hatching, and females spend more time resting at nest. Later, females increase their foraging and by time chicks well-grown sexes sharing work about equally. Around fledging time parents forage simultaneously; often roost away from nest.

BEHAVIOUR OF YOUNG: No noteworthy details.

FLEDGING: Fledglings typically depart during morning. Form groups of juveniles and return to nest to be fed (late afternoon). Eventually forage with small groups of adults. Fledging period 40–5 days.

POST-FLEDGING: Continues to be fed even more often than before fledging. Female provides more than male thereby, perhaps, making up for his earlier investment surplus and thus ensuring parity in their eventual physiological fitness.

Period unknown. Reportedly young of previous season tend still to associate with parents at start of next breeding season.

BREEDING SUCCESS: At Anvers Island, 1978–80 fledging success 44–82%. In 1978–79 many nests fledged 3 chicks but in 1979–80 many fledged only one or none.

FIDELITY TO COLONY, SITE, AND MATE: Although pedestals persist from year to year and strong tendency for birds to re-nest within same part of colony, actual site and mates often changed; despite fact that under suitable conditions birds remain on territories throughout winter. Of 12 pairs in which both partners survived 7 had different mates in successive seasons.

AGE OF FIRST BREEDING: 4–5 years.

NON-BREEDING YEARS: No details.

LONGEVITY AND MORTALITY: At Anvers Island of 30 pairs 18 individuals disappeared, presumed dead, between 1979 and 1981, annual adult mortality of 10% if 3 full seasons were involved or 15% if only 2 years.

South Georgia(n) Shag *Phalacrocorax georgianus*

PLATE 8

Phalacrocorax atriceps georgianus Lonnberg, 1906, South Georgia.

Often considered race of *P. atriceps*. Some authors give specific status to population of South Georgia but refer related forms from other regions to *P. bransfieldensis*. Sometimes put in genus *Notocarbo*.

Other common names: none, except that, where it has been referred to as part of the Antarctic blue-eyed shag complex, then the common names used for this group may have been applied. Thus Shaw (1985a, 1985b) in detailed study on Signy (South Orkneys) refers to it as the blue-eyed shag *P. atriceps bransfieldensis*.

French: cormoran Georgien. German: Sudgeorgienscharbe. Spanish: cormoran de Georgia.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Forehead, crown, hindneck black with blue gloss; bottom edge of black cap starts just below eye, passes through ear-coverts. Black crest on forehead rather ragged; c. 5–6 cm long. White filoplumes above and behind eye. Green sheen on black upper wing coverts; scapulars sharply distinct from blue gloss on mantle. White patches on wings often prominent but sometimes small or absent. White patches on back may be absent or hidden by wings. Underparts white, tail, thighs black. Dark-coloured bill sports two prominent yellow caruncles above base. Eye brown with ultramarine blue ring. Face, throat dark. Legs, feet pink with some black on legs.

ADULT F: Similar.

POST-NUPTIAL: Plumage becomes faded; soft parts dull; crest disappears.

JUVENILE AND IMMATURE: Dull brown where adult black. Juvenile bill light grey-brown with darker ridge and lighter tip. Lacks caruncles; this area purplish and papillated. Eye light brown. Legs, feet pink. Post-juvenile, eye-ring dull blue.

Field characters

No other shag has been reported from South Georgia and other islands of Scotia Arc but on plumage alone this shag would be doubtfully distinguishable from close relatives. However, demarcation between black cap and white cheeks passes through ear-coverts whereas some populations of *bransfieldensis* have white cheeks (*atriceps* of some classifications) and others have black (*albiventris*).

Measurements (see Appendix)

Voice

Probably as for Antarctic shag; male rough call, female hiss. Chicks utter repetitive low whistle.

Range and status (Figure 6.134)

Islands of Scotia Arc including: South Georgia, South Orkney (which includes Signy Island) and South Sandwich. Population probably fewer than 9,000 pairs. On South Georgia itself many small colonies of considerably fewer than 100 pairs, many only 10–20, together totalling fewer than 4,000 pairs. South Sandwich 100–1,000 pairs, South Orkney 10 colonies holding in total perhaps 2,000 pairs of which Signy has 830 pairs (Prince and Croxall 1983; Croxall *et al.* 1984; Shaw 1986). Colonies fluctuate in size from year to year.

MOVEMENTS: Resident; limited local movement.

Foraging and food

(Wanless *et al.* 1992, Wanless and Harris 1993, Wanless *et al.* 1995 refer their observations to *P. atriceps*, but at South Georgia, so *P. georgianus* in this classification.)

In main, birds fed solitarily, close inshore, or in small groups, often 10–20, but no evidence of cooperation. Spends 75% foraging time submerged (juveniles bit less than adults). In deep water descended near-vertically after preparatory upward leap. Wanless *et al.* (1992) found that at South Georgia individuals frequently remained submerged for more than 3 min searching among kelp, and reached depths of more than 80 m, with individual differences in diving pattern and performance. Same individual, on same day, showed ‘short’ dives (<120 sec) and ‘long’ dives (>120 sec). Dives lasted av 28 sec, recovery time 10 sec. During chick-rearing made 2.3 feeding trips per day, female making first one. Av absence 6.22 hr per day. During feeding, 86.7% of time spent diving but long periods of recovery on surface and this, together with time spent travelling to seabed meant only 1.06 hr per day available for capture of prey (Wanless *et al.* 1995). Although parents of broods of 2 or 3 chicks spent 6.42 hr per day diving, against only 4.74 for parents of single chicks, diving time did not increase as chicks grew larger. Interestingly, Wanless and Harris (1993) found that shags from groups as near to each other as 2.5 km nevertheless used different feeding areas, with no overlap. Takes mainly fish, principally *Notothenia rossi* but also other species of this genus. On Signy, *N. nudifrons* contributed 75% of prey by weight. Casaux *et al.* (1997b) for *P. bransfieldensis* (South Orkneys) record fish, mainly *Notothenia coriiceps*, main prey followed by octopods, decapods, and gammarids. Takes fish up to 27 cm weighing up to 201 g (see also *P. bransfieldensis*). Females made first feeding trip of day in 93% of pairs; each bird made av 2.3 trips per day, total absence of 6.22 hr per day (Wanless *et al.* 1995). Birds with 2 or 3 chicks dived 1.68 hr per day more than those with 1 chick.

Habitat and breeding biology

(See Fig. at end of ch. 5; Shaw 1985a, 1985b, 1986; Marchant and Higgins 1990; Extensive detail in Johnsgard (1993), under *Leucocarbo atriceps* lumps data from *bransfieldensis*, *georgianus*, *melanogenis*, *verrucosus*, *nivalis* and *purpurascens*)

HABITAT: Most comments made for Antarctic shag apply here. On Signy some nests built on snow and

ice. Nests on flat or sloping ground often amongst tussock grass and on ledges of precipitous cliffs facing sea.

COLONIES: Groups <100; on Signy 0.7 nests per m²; centre pairs strong site fidelity.

FREQUENCY, TIMING, AND DURATION OF BREEDING: No evidence of double broods, though closely related imperial shag said sometimes to breed twice within a year. Spring breeder although return to colony may be severely disrupted by bad weather. At Signy, Shaw (1985b, 1986) found that some adults acquire breeding plumage by mid-May although mid-July before return to colony. Even July is substantially before courtship begins in early Sept followed by nest-building and first eggs late Oct-early Nov. At South Georgia first eggs appeared second part Nov or early Dec. Eggs hatch Jan and chicks leave nest in March. Thus breeding season protracted and few weeks of year in which no adults either in nuptial plumage or breeding. Nevertheless, laying fairly well synchronized (24–35 days on Signy). Average date first eggs over 16 years 1 Nov with variation of 6 days. Apparently unrelated to wind temperature or snowfall. Clutches of 3 started av 4 days earlier than clutches of 2.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Mutually displaying partners repeatedly lower heads first on one side, cheeks touching, then on other, continuing for minutes. ‘Circle flying’, common in cormorants though neglected in species accounts, occurs in this shag (Marchant and Higgins 1990).

Breeding behaviour largely undescribed. Displays assumed similar to other blue-eyed shags.

NEST: Steep-sided truncated cone with small, deep cup. Height 20–5 cm. Sometimes on top of dead tussock. On S Sandwich entirely penguin tail feathers.

EGG/CLUTCH: (Shaw 1985a, 1986) 62.4 × 39.9 n = 333 Signy Island. 1st and 2nd eggs from clutches of 2 and 3 measured 62.5 × 39.9

$n = 254$, whereas egg 3 measured 62.1×39.6 $n = 79$. Yolk comprised 18.2% by weight of egg contents and 15.7% of whole egg, wet weight. Proportion of albumen increased with size of egg but that of yolk decreased. Hence smaller eggs contained proportionately more yolk. Clutch usually 3. Signy av clutch-size 2.31 $n = 37$ (1979), 2.64 $n = 687$ (1980). In 1981, however, 2.84 $n = 508$; proportionately more clutches of 3 than in the other years (64% in 1979 and 1980 combined, 88% in 1981). Within clutches of 3 mean laying interval egg 1–egg 2 shorter than egg 2–egg 3. Egg 3 laid 5 days after egg 1. Shaw examined eggs 1, 2, and 3 of 3-egg clutches for volume, laying, and hatching weights to determine whether these affected survival of chicks (see below). Whilst no significant difference in volume of egg 1 and egg 2, third egg 2.3–3.7% smaller and therefore lighter. This difference affected hatchling's weight. At birth, chicks from egg 1 and egg 2 similar (hatchling from egg 1 of 2-egg clutch weighed 39.4 ± 4.88 g against egg 2's 42 g ± 2.56). For clutches of 3, hatchling from egg 1, 40.1 ± 4.44 g; egg 2, 40.1 ± 3.76 , egg 3, 36.2 ± 3.72 .

REPLACEMENT LAYING: Clutches lost early enough may be replaced.

INCUBATION: Usually c29 days (27–31 depending mainly on laying order). Eggs hatch asynchronously, producing much greater differences in weights of siblings than does differences in egg-size. In clutches of 2 laying interval 3 days, hatching interval 2 days. In clutches of 3 interval between successive eggs 2.6 days, hatching interval just under 2 days. Presumably egg 1 only partly incubated during interval between it and egg 2, whereas eggs 2 and 3 incubated from day laid.

Females aged 10–11 years showed laying intervals shorter than those of 3–9 year-olds. Moreover egg 3 of older females 'caught up' during incubation more than those of younger females, probably because former more efficient incubators. Importantly, growth and survival of chicks (below) reflected hatching asynchronies. Shaw suggests that

smaller and later-hatched 3rd egg may be adaptive in facilitating brood reduction.

CHICK/BROOD: Hatchling black skin, pink throat, blue mandibles; grey legs, feet. Down appears c. 10 days, covers chick by day 14; blackish with few white filoplumes.

Shaw (1985a) provides more detailed analysis of development and survival of chicks from eggs 1, 2, and 3 than available for any other phalacrocoracid. Within 24 hours of hatching, egg 1 chicks from clutches of 2 weighed 39.4 ± 4.88 g against 41.2 ± 2.56 for egg-2 chicks. From clutches of 3, egg-1 chick 40.1 ± 4.44 ; egg-2, 40.1 ± 3.76 , egg-3 36.2 ± 3.72 . When chick 3 hatched, chick 1 already twice as heavy. On day 5 chick 3 only c33% weight of chick 1, c50% chick 2. By time chicks attained asymptotic weight chick 3 was 300 g lighter than chick 2 and 390 g than chick 1 (weights: chick 1, 2,530 g; chick 2, 2,440 g, chick 3, 2,140 g). Asymptotic weights of chicks 1 and 2 from broods of 2 no greater than from broods of 3, clearly indicating that any shortfall in food fell on chick 3. However, single chicks did reach higher asymptotic weight than chick 1 from broods of 2 or 3, indicating that presence of even one sibling significantly affected chick 1's weight just prior to fledging, though any reproductive disadvantage thereby offset by extra productivity. In broods of 2 and 3, chick 1 achieved significantly heavier asymptotic weight than chick 2. Their asymptotic weights, respectively, 1.18 and 1.14 times greater than that of chick 3. Thus in normal asynchronous broods of 2 or 3 at least one 'heavy' chick is produced, which may be adaptive since chicks heaviest at fledging probably survive best. Nevertheless Cobley (1989) reported no significant differences in proportions of 1st, 2nd or 3rd chicks, ringed 1969–83 and recaptured 1987, implying that survival uninfluenced by 1st, 2nd or 3rd status.

Shaw's results, above, refer to normal, a-synchronous broods but he created some synchronized broods by manipulation of eggs. In such broods, more cases in which *all* chicks died. In

normal broods chick 3 died (89% mortality against 16–22% for chicks 1 and 2). Note, though, that chick 3 not inherently less viable than chick 1 or 2. If egg 1 or 2 fails to hatch, chick 3 survives as well as 2nd-hatched chick in normal brood of 2. Age at which potential replacements die is relevant, since the longer they live and the more investment they absorb, perhaps to detriment of siblings. Av age at death of chick 3 (15.4 days) 24 days earlier than that of chick 1 (39.6 days) ; chick 2 was 33.7 days. However, chick 3 managed to survive longer if parents 'old' (6–12 years) than if 'young' (3–5 years), presumably because more experienced adults delivered more food to brood, thus leaving more for chick 3.

Shaw estimated weight of feeds delivered to chicks days 1–65. Sigmoidal pattern resembled that of brood-weights. Food weight greater for broods of 3 than of 2, and of 2 than for single chicks. Between day 1 and 10 mean weight of feeds (per brood) increased 30-fold. By day 41–65 broods of 3 received >2000 g per day. Chicks receive individual feeds of less than 10 g during first 10 days, rising to 20 g days 11–20, c50 g days 31–40 and (max) 120 g after day 41.

Although mortality of chick 3 highest day 1–10, amount of food eaten by broods of 3 at that time is mere eighth of amount which, later (days 31–40), brood of 2 chicks will consume. Suggests parents deliberately withhold food from chick 3 (unlikely) or that sibling competition responsible for its death even though adults theoretically capable of bringing enough food for all. However, adults will not bring as much food to 3 small chicks as, later, they will bring to 2, or even 1, large chick. So chick 3 will inevitably have to compete for limited amount of food brought. Within broods of 2 each chick received about an equal number of feeds whereas within broods of 3 smallest chick got fewer feeds. Days 11–15, lightest chick received only 12% of all feeds brought. Thus its effect on other two slight and whether it survived or not made no significant difference to asymptotic weight of chicks 1 and 2.

CARE OF YOUNG: Attendance decreases as chicks grow and as they approach fledging are usually unattended.

FLEDGING: Young leave nest c40–5, days usually in morning, and join group of juveniles, but return to nest for feeds, usually in afternoon. Fed more often than before, especially by female. Fledging period c. 8 weeks. On Signy c65 days.

POST-FLEDGING: Duration of feeding unknown. By mid-Feb have joined small foraging groups of adults.

BREEDING SUCCESS: (Signy, Shaw 1985a) Hatched from laid: 85% (n = 645), 91% (n = 633). Fledged from hatched: in normal broods of 3, 59.7% (n = 82, 1980), 78.9% (n = 125 1981); not significantly different from those of equivalent-sized broods which had been experimentally manipulated to synchronize ages of chicks. Late breeders produced 0.65 chicks per pair fewer than early breeders.

FIDELITY TO COLONY, SITE, AND MATE: Fluctuations in numbers at individual colonies implies fairly low fidelity to breeding group, and therefore to nest-site and mate. In fact 77% of birds change mates in successive seasons; 56% through death or disappearance of previous partner; only 44% by divorce, both partners being alive and within colony. Contrary to many seabirds, likelihood of partners remaining together not affected by success or failure of previous breeding cycle.

Within group whose members 3–12 years old, 29% of birds had partners of same age; after dissolution of pair-bond 41% of new pairs had equal-aged partners whilst 31% had partners differing by one year, younger of pair being failed breeder of previous year (Shaw 1985b). He suggests partners select on basis of age though unable to say what behavioural or physiological cues might be involved.

AGE OF FIRST BREEDING: 3–4 years.

OTHER ASPECTS: No details.

Heard Shag *Phalacrocorax nivalis*

PLATE 8

Phalacrocorax (Leucocarbo) atriceps nivalis Falla, 1937, Heard Island.

Often considered race of *Phalacrocorax atriceps* complex; sometimes placed in *Leucocarbo* or *Eleucocarbo*.

Other common names: Included among blue-eyed shags or cormorants.

French: cormoran de Heard. German: Heardscharbe. Spanish: cormoran de la Heard.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Large, noticeably white shag. Forehead, crown, hindneck black with blue gloss. White on face conspicuous because extends obliquely upwards from eye, leaving cheeks and ear-coverts white. Black, recurved crest on forehead, tuft of white filoplumes above and behind eye and scattered on head, neck, back. Back black with pair of white patches in middle. White alar bar and scapular patches usually very conspicuous but may be small or absent. Rump, tail black; underparts white. Underwing black with variable white axillary line along humerus. Bill grey with horn-coloured patch at tip of lower mandible, conspicuous pair of orange caruncles, orange skin at base of lower mandible. Blue eye-ring. Pink legs, feet.

ADULT F: Similar.

POST-NUPTIAL: Loses crests and plumes, caruncles become yellow, dorsal plumage, soft parts fade.

JUVENILE AND IMMATURE: Brown with green gloss on upperparts, white beneath and on neck though dark-faced. Alar patch variable in size, pale brown. No blue eye-ring; caruncles absent.

Field characters

Larger than most blue-eyed shags (though smaller than *bransfieldensis*) with whiter cheeks but only shag on Heard Island. Walks a great deal.

Measurements (see Appendix)

Voice

Loud 'brah-brah' or honk (male), hiss (female).

Range and status (Figure 6.134)

Mainly restricted as breeder to NW coast of Heard Island but breeds (up to 55 nests) Stephenson Lagoon area on E. Population appears to fluctuate but may be only 600–1,000 birds. Since 1950s max breeding population c90 pairs, commonly fewer than 40; max chicks fledged 1986, 87, 88 was 43, 7, 94. Max number birds at main roost (Stephenson's Lagoon) declined from 548 to 127 (1985–88) (refs in Marchant and Higgins 1990). Seems total population decreased from 600+ to c250 in 8 months, 1987, possibly result of single event (Green *et al.* 1998). Latest figures (Green 1997b, Green *et al.* 1998) show max count 1992–93 135 juveniles, 309 adults. Vulnerability of this small population and lack of legal protection causes concern.

MOVEMENTS: Local.

Foraging and food

(See Green and Williams 1997)

Generally inshore in shallow water singly or in small groups. In fine weather in winter leaves roost within 60–90 mins of first light but may not depart till afternoon. Early in breeding season departs before dawn. In 3 breeding pairs with recorders attached, female first to go foraging each day (number of foraging bouts per day, both sexes, varied 1–4). On av, first dive occurred 70 ± 57 min $n = 12$ after sunrise. Males and females alternated in foraging bouts. Male

foraging ended later than female, av 57 ± 51 min $n = 25$ before sunset. 27 non-breeders (Feb) began 4 hr 22 min ± 56 min after sunrise, ended 2 hr 48 min ± 69 min before sunset, giving av daily foraging 7 hr 31 min ± 64 min (not continuous). Breeding females dived 65.1 ± 19.6 times per day compared with 48.7 ± 16.4 for males, but time spent submerged (128.5 ± 17.8 min for females against 106.3 ± 15.0 for males) did not differ significantly. Breeders spent significantly more dry time (272.5 min) per day than non-breeders (47.0 min). Shallow dives, mostly 2 m or less, accounted for half those measured, with few between 6 and 10 m. Most dives greater than 5 m terminated between 16 and 40 m. Deepest dive 60 m though up to 150 m suggested (Marchant and Higgins 1990).

Food consists largely, though variably in different years, of polychaetes (thought to be *Eulagisza corrientis*) and small notothenid fish of 4 species, with a few octopods, limpets, and isopods. Unusually high incidence of polychaetes taken by all birds in non-breeding season, found in virtually all pellets and making up most of remains at roosts. They estimate colony takes 126 tonnes polychaetes a year, including breeding. However, birds feeding chicks change to diet of fish, presumably because more nutritious. Suggested that local availability of fish may help determine where breeding colonies situated on Heard Island.

Habitat and breeding biology

(See Fig. at end of ch. 5; Green 1997b; extensive detail in Johnsgard (1993); under *Leucocarbo atriceps* lumps data from *bransfieldensis*, *georgianus*, *melanogenis*, *verrucosus*, *nivalis* and *purpurascens*)

HABITAT: On sea-facing cliff-tops sometimes among tussock grass but also on weathered lava surrounded by glaciers.

COLONIES: Precise area changes from year to year. Only 2 small breeding colonies recorded by Downes *et al.* (1959); volcanic promontory and offshore stack. Latter moved to main island cliffs. Av min distance between nests 48 cm.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually. Observations at Stephenson's Lagoon showed pairs began forming mid-July, first copulation 15 July. First egg 2nd week Sept (but first chick 30 Oct; odd since incubation period c30 days). Laying continued till 21 Nov. Mean laying date 11 Oct ($n = 34$ eggs) though variable; in some years earliest egg not until early Oct and most eggs not until late Oct. Mean hatching date 11 Nov (28 Oct–17 Dec). For an individual pair, 4–5 months can elapse between first signs breeding activity and egg-laying. Adults deserted colony at night by 22 Feb and joined roosts of non-breeders on beach. Duration complete breeding cycle—egg laying to independence—c. 16 weeks but from initial breeding activity to independence of young some 36 weeks.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: (Similar to *P. atriceps*, Green 1997a) 'Circle-flying' uncommon; no extended fights. Allo-preening (unilateral and mutual).

COPULATION: (GFA)

NEST: Approx 22 cm high. Distance between nests 47.6 ± 10.8 cm $n = 10$. Mainly tussock grass *Poa cooki*, compacted mud and guano. Does not use seaweed. Collects material by flying 100–50 m from site or walking up to 50 m. May transport large loads. Pilfers unattended nests enthusiastically; tolerated by near neighbours but threatened if stealing further afield. Both partners handle and build-in material.

EGG/CLUTCH: $63.6 (58.7–69.5) \times 40.3 (36.9–42.8)$ $n = 107$. Volume 52.6 ± 3.4 cm³ (amongst highest recorded for blue-eyed shag group; cf. 46.1 *P. melanogenis*, Marion Island, Rand 1954). Clutch mean size 2.8 ± 0.4 . No 4-egg clutches found in Green's study though elsewhere 4 given as usual clutch-size. Egg-size marginally decreased from 1st to 3rd egg. Eggs 1 and 2 similar but 3 significantly smaller (1.5 cm less in volume). Between laying of successful eggs 1 and 2, 3.3 ± 2.5 days elapsed (range up to 9 days) but eggs can be laid

less than 24 hours apart. Mean interval between eggs 1 and 2 unusually long, possibly due to comparatively large volume of eggs. On av egg 1 hatched c. 1 day before egg 2 and egg 2 2.5 days before egg 3, but eggs 1 and 2 occasionally hatched on same day.

REPLACEMENT LAYING: Occurs; no details.

INCUBATION: 28 days eggs 2 and 3 (26–30) $n = 13$; c30 days egg 1 (29–32) $n = 14$.

CHICK/BROOD: (Growth in Green 1997b) Hatchling naked. Downy by day 9; brown with scattered white plumules on ventral surface. Down thick and woolly on head, looser on back. Weight increases rapidly from day 5, reaching adult (c. 2,750) from day c50. First unattended c39 days Chick 1 not significantly heavier than chick 2 up to 25 days but from day 35, paradoxically, actually lighter than chick 2 and this persisted up to day 55 when weighing ceased. Yet at day 55 chick 1's longest primary longer than that of chick 2. Thus mass and longest primary told different stories. Chick 3 at 55 days as heavy as chick 1, which means that, whether or not chick 3 can be regarded as an insurance, if it survives it grows as well as chick 1 in a good food year. Tarsus and middle toe achieved adult length by day c35, culmen reached min adult length by day 45, but by day 55 wings still shorter than adults'. Of 26 nests 4 held 3 young, 15 held 2, 7 held 1 (av brood size 1.9).

CARE OF YOUNG: Adults leave chick unguarded at c39 days. Those with broods of 3 spent less time at nest than those with 2, thus apparently matching food-gathering effort to brood-size. Once young have left nest adults feed them within colony area.

BEHAVIOUR OF YOUNG: Move off nest c30 days, wing-exercise 34 days, wander c41 days. Practice-flying (not full) observed 55 days. About month later observed moving on foot towards main feeding area. After further month (now end Feb) seen

flying towards feeding area. Chase parents for food.

FLEDGING: Period very approximately 55 days.

POST-FLEDGING: Fed; no details.

BREEDING SUCCESS: Hatched from laid: no straight figures available—of 140 eggs laid in 50 nests, 1992–93, 82 chicks fledged, but this loss includes chick deaths. Of eggs that did not produce fledglings, 52 failed to hatch, though incubated, 6 from abandoned nests, 8 broken. Fledged from hatched: (number unstated) only 12 died before fledging. Of these, 7 died at days 1–5, remainder days 7–10. Fledged from laid: 58.6% ($n = 140$). Elsewhere, Green gives breeding success as 62.6% for control group and 66% for group in which chicks handled. Insignificant correlation between position of egg in clutch or number of chicks in brood and likelihood of fledging. Breeding success of late clutches $n = 6$ only 25% compared with 61.7 for earlier clutches. Fledged per nest with eggs: c. 0.5 (1985–86); c. 0.3 (1986–87); c70 chicks from 100 nests (Feb 1988); variable but often low (0–100+, Green *et al.* 1998); 1.89 (some pairs raising 3 chicks with high subsequent survival, Green 1997b).

FIDELITY TO COLONY, SITE, AND MATE: No details concerning marked birds breeding in different parts of island.

AGE OF FIRST BREEDING: No information.

NON-BREEDING YEARS: No information.

LONGEVITY AND MORTALITY: Indications that in some years juveniles may fare badly. However, in May 1992 135 juveniles counted and 133 counted at roost in Dec, indicating extraordinarily high survival through winter if 135 represented total number alive in May. 1993 also apparently a productive year, so that poor reproductive performance in previous years may be compensated for. No information on adult mortality rates.

Crozet Shag *Phalacrocorax melanogenis*

PLATE 8

Hypoleucos melanogenis Blyth, 1860, Îles Crozet.
Often considered race of *Phalacrocorax atriceps*.

Sometimes placed in *Hypoleucos* or *Notocarbo*.

Other common names: Marion Island shag.
French: cormoran de Crozet. German: Croz-
etscharbe. Spanish: cormoran de las Crozet.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Top of head, sides and back of neck black with blue gloss. Black recurved crest on forehead. Throat, sides of neck, underparts white. Boundary line between black cap and white neck and face extends from gape to below ear-coverts, then down sides of neck, leaving only lower cheeks and throat white. Large tufts white filoplumes behind and above eye, scattered on head and neck. No white patches on black back, although usually narrow white alar bar. Wing-coverts, scapulars black with bronze-green sheen; rarely white patches on scapulars. Wings brownish-black but tail-feathers black. Underwing blackish with variably long white humeral line. Bill black or greyish maybe with light brown tip to upper mandible, prominent orange caruncles at base. Gular pouch black or grey with conspicuous yellow spots often extending onto base of lower mandible. Eye-ring iridescent blue, eye brown. Legs, feet pink.

ADULT F: Similar.

POST-NUPTIAL: Crest and plumes disappear, plumage fades, caruncles yellow.

JUVENILE AND IMMATURE: Juvenile dark brown above without white alar bar; white below. Gular pouch violet with black posterior border. Eye,

eye-ring brown. Immatures develop sandy alar patch; may have brown blotches on ventral surface. Face turns yellow. Legs, feet pink.

Field characters

Only shag present in Crozet Archipelago, including Prince Edward and Marion Island. Closely resembles Macquarie shag *P. purpurascens* and Kerguelen *P. verrocous* but former shows larger white alar and scapular patches; latter smaller, with black on head extending lower on cheeks.

Measurements (see Appendix)

Voice

Male utters repetitive 'egh-egh-egh' or 'heh-heh-heh' during display. Threatens with drawn-out 'whaah'. May 'tick' before take-off; barks loudly during kink-throat and male 'roars' after hop. Both sexes make loud 'kok-kok' before regurgitating pellet. Female hisses during gape-display.

Range and status (Figure 6.134)

Endemic to Crozet, Marion, and Prince Edward Islands (Marchant and Higgins 1990).

MOVEMENTS: Local. Colonies never entirely deserted.

Foraging and food

(Cooper 1985c; Marchant and Higgins 1990)

Inshore shag of sub-Antarctic waters, rarely out of sight of land, often feeding on edge of kelp beds or within 1 m of shore in breaking waves, though very rough weather may inhibit feeding altogether. Will venture several km offshore. Before foraging, birds usually bathe and head-dip. Usually forage singly but sometimes in groups which may dive synchronously. Duration of dives 68 sec (45–95) $n = 6$ Îles Crozet, 46 sec (28–69) $n = 27$ Marion. Max 88 sec recorded. At Prince Edward Islands

Cooper (1985b) found that dives averaged 40 sec though some took as long as 88 sec. Two foraging bouts lasted 50 and 56 min during which birds underwater 68% of time, resting on surface 26%; remainder bathing, preening and flying. Food mostly fish; some crustacea, mainly shrimps, octopods, benthic invertebrates. Around Marion Island *Notothenia squamifrons* formed 71.4% by mass of diet, av 5.3 cm (2.3–10.9) all juvenile; av weight regurgitated boluses 58 g (11–310) $n = 47$ (Espitalier-Noel *et al.* 1988). This fish pelagic for its first year but may then be restricted to bottom waters. Also takes *Paranotothenia magellanica* av 11.5 cm (8.8–20.2), weight 53 g (0.5–201.6). Fish least important food-items April–May (46% weight), most important Feb–March (97%). Crustacea, principally *Nauticaris marionis*, though small (av 29.5 mm) comprised 18.8% of mass taken. This crustacean occurs commonly at 30–270 m around Marion. On Crozets, prey various demersals, mainly notothenoids (*Lepidonotothen*, *Paranotothenia*, *Dissostichus*, *Nothothenia*, *Harpagifer*). Also invertebrates including polychaetes (Ridoux 1994).

Habitat and breeding biology

(See Fig. at end of ch. 5; Derenne *et al.* 1976 (Crozet); Williams and Burger 1979 (Marion); extensive detail in Johnsgard (1993) under *Leucocarbo atriceps* lumps data from *bransfieldensis*, *georgianus*, *melanogenis*, *verrucosus*, *nivalis* and *purpurascens*)

HABITAT: Coastal cliffs, up to tens of metres above sea level, or on vegetated slopes among tussock grass, or on rocky outcrops. Occasionally in caves or on boulder beaches.

COLONIES: Up to c50 nests though 57% <10 pairs, only 20% >20 nests (Crozet). On Marion colonies av 24 nests (6–51). Nests may be extremely close-packed.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually, but suspicion (no more) that very early breeders may be double-brooded. Courtship begins early Aug, nest-building Sept and attendance increases until site permanently occupied

during last 3 weeks before laying. Commencement of egg-laying at Îles Crozet mainly 25 Oct–13 Nov (earliest 12 Oct) and last clutches varied, according to year, from 3 Dec–1 Feb. Thus egg-laying as a whole may be protracted, though concentrated heavily in one part of entire period (67% laid 13 Nov–12 Dec). Late eggs probably replacements or attempts of first-time breeders. At Marion Island 50% of eggs laid by 11 Nov. Thus given a 28-day incubation period, most eggs on Îles Crozet hatch Dec–Jan, followed by fledging in Feb–early March though juveniles do not leave colonies until late April or early May. On Marion Island colonies almost deserted by March. On Prince Edward Island, at least in some years, breeding may be much earlier—in 1984 some laying occurred in mid-June.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Nest-site defended by threat and aggressive calling. In male sexual advertising head swings back in vertical arc and as nape touches back (no head-rotation) loud, short call uttered whilst base of neck pulsates and foreparts rise and fall. Tail raised to 45° and wings droop. During pair-interactions partners may gape, forwards, sideways, upwards, with S-shaped neck and horizontal body. Males call repetitively and females hiss. Partners, standing parallel with throat kinked, lower and raise head, often simultaneously. Before take-off bill slightly opened, base of neck pulsates, and tail lowered; male ‘ticks’ and female utters soft, repetitive call. Once airborne, male may roar. This ritualized behaviour may be repeated and between times either sex may make contact with partner’s head, using open bill, though apparently not overtly aggressive. On arrival with nest-material, birds kink-throat in upright posture or with retracted head, usually silently though male may roar. In ritualized walking (penguin-walk) neck arched and closed bill points down and is pressed against neck (NB: Fig. 68 in Marchant and Higgins disagrees with their text). It resembles pre-hop posture in which neck strongly arched and bill pointed down. During hop male may tick and then roar whilst female silent or calls softly.

COPULATION: (GFA)

NEST: Site selected by male who brings most or all material mainly *Cotula plumosa*, with grass, seaweed, and debris. Cemented with guano. Cone up to 20–5 cm high. Both partners build (mainly female) and guard; pilfering common. Usually newly built each year.

EGG/CLUTCH: 64.4 (58.6–70.3) × 39.5 (37.6–41.8) (n=20 Crozet); 62.9 (58.5–69.8) × 39.6 (35.6–43.5) (n=145 Marion). Weight: 59 (57–61) (n=3 Crozet); 53 (43–63) (n=139 Marion). Clutch: 2.9 (2–5) (n=20 Crozet); 2.6 (1–4) mostly 3 (n=41 Marion). Laying interval av 2.9 days egg 1–egg 2; 2.8 days egg 2–egg 3 (Marion).

REPLACEMENT LAYING: ‘Occasional’. In one case, young taken by predator 13 Jan and replacement clutch laid 18–19 days later.

INCUBATION: Shared. Probably, full incubation starts after laying of egg 2. Period av 28–9 days (27–31). Shifts c. 12 hours.

CHICK/BROOD: Hatch a-synchronously; interval one day from egg 1–egg 2, 3–4 days egg 2–egg 3. At Îles Crozet hatching of all eggs in clutch av 1.6 days (1–3), at odds with figure of 3–4 days (above) between egg 2 and egg 3. Hatchling blackish. Grey-brown down appears day 8–14. Day 16–25 wing and tail-feathers erupt gradually followed by contour feathers. Down may persist on head and neck until day 65. Hatchlings fed during first day and then usually several times a day (c. 3–4 hours if 2 chicks). Within 24 hours of hatching chick weighs 40.4 g (38–45) n=17. Chick 1 significantly heavier than chick 2 or 3. Weight increases linearly for 45–50 days. Îles Crozet max weight 2,345 g (2,100–2,650) n=20, reached on av day 46 but as early as day 34 or as late as fledging day. At Marion Island max weight 2,487 g was 117% of mean adult weight and attained at c60 days. Whereas wings increase in length av 25% every 5 days until fledging, legs and feet fully-grown at c30 days thus enabling chick to leave nest before it can fly. No significant difference in growth

between chicks 1 and 2 but chick 3 under-nourished; usually dies after few days.

CARE OF YOUNG: At first, brooded continuously, parents taking alternate shifts for first 18–19 days. Then attended intermittently until 31–44 days or sometimes until they fledge. Male takes greater share in feeding young (61% against 39%).

BEHAVIOUR OF YOUNG: Chicks thermoregulate by c. 18 days. Begin to wander days 31–44 even taking to water, swimming and diving, though at this stage some down may remain on head and neck (could these have been escaping disturbance?).

FLEDGING: Period 56 days (50–63) n=19 but figure arbitrary; some young birds not fully capable of flight even at 80 days.

POST-FLEDGING: Even after leaving area of colony young still partly depend on parents for food for about a month, coming to land to be fed.

BREEDING SUCCESS: Hatched from laid: 65%, 56% (2 years, Crozet). Kelp gulls responsible for most egg loss in first 2 weeks of incubation (how did they gain access?). 62%, 45% (Marion); egg-loss caused by high seas (39%), failure to hatch (37%), disappearance (24%). Predation negligible. Fledged from hatched: 22% (Marion, 10% starvation during high seas, but sample low); 59%, 54% (Crozet, 40% starvation, 33% skuas, 6% giant petrels, losses mainly at 20–30 days. 71% chicks from egg 1 survived, 64% chicks 2, no chicks 3). Fledged from laid: 39%, 31% (2 years, Crozet); 88–100% clutches laid after 1 Jan failed; 55% laid before 20 Dec.

FIDELITY TO COLONY, SITE, AND MATE: At Crozet pair-bond apparently lasts only one season; none of 4 pairs studied retained previous partner.

No information on age of first breeding, mortality rates etc.

Kerguelen Shag *Phalacrocorax verrucosus*

PLATE 8

Halieus (*Hypoleucos*) *verrucosus* Cabanis, 1875, Îles Kerguelen.

Sometimes placed in *Halieus*, *Hypoleucos* or *Notocarbo*.

Often considered race of imperial shag *P. atriceps*. Suggestion that individuals of *P. melanogenis* or *P. nivalis* might have recently arrived in E Kerguelen and hybridized with local birds (see 'plumage').

Other common names: Kerguelen cormorant.

French: cormoran des Kerguelen. German: Kerguelenscharbe. Spanish: cormoran de Kerguelen.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Head, hindneck deep blue or purple; black crest on forehead; black cap extends from chin, below eye-level to ear-coverts, giving dark-cheeked appearance. Back, wing-coverts, scapulars, tail, thighs greenish black. White alar and back patches usually absent but proportion bearing these features varies throughout population (see Derenne *et al.* 1976; Weimerskirch *et al.* 1989). Throat, foreneck, underparts white. Underwing brown. Yellow to orange caruncles above base of brownish or horn-coloured bill. Gular pouch and face dark brown with yellow-orange tubercles. Eye hazel, eye-ring bright blue. Legs, feet dark brown to bright pink with dark blotches.

ADULT F: Similar.

POST-NUPTIAL: Plumage becomes faded, caruncles diminish and turn dull yellow, eye-ring becomes lead-blue. Crest disappears.

JUVENILE AND IMMATURE: Juvenile dark brown upperparts, variable amount brown and white on underparts, no facial caruncles. Iris brown, eye-ring lead-blue, bill and feet brown. Immature gradually

acquires metallic gloss on upperparts, more white on underparts. Light and dark colour morphs distinguished in some immatures.

Field characters

Smallest blue-eyed shag; black above, white below with black cap even lower on cheek than Crozet shag—below angle of gape.

Measurements (see Appendix)

Voice

Male raucous growl, hoarse croak, female hisses (details lacking).

Range and status (Figure 6.134)

Endemic to Kerguelens. Found at sea throughout archipelago usually <6 km from shore. Population c. 6,000–7,000 pairs, 1984–87. Watson (1975) suggests Kerguelens reached by Heard shags and hybridization gave range of plumages (white alar bar on some).

MOVEMENTS: Local.

Foraging and food

Forages inshore in bays and other inlets though immatures recorded out to 80 km on Kerguelen shelf. During summer feeds among kelp, sometimes on bottom. Occasional scavenger around boats. In Jan–Feb feeds mostly solitarily but May–Oct may feed communally and possibly cooperatively in flocks of several hundreds, apparently forming a long line in which birds dive and surface in progression along row. Food presumed to be mostly fish and benthic invertebrates (echinoderms, crustacea, polychaetes). Johnsgard (1993) for imperial shag, includes *verrucosus*.

Habitat and breeding biology

(See Fig. at end of ch. 5; Marchant and Higgins 1990, quoting van Tets; Stahl; Extensive detail in Johnsgard (1993); under *Leucocarbo atriceps* lumps data from *bransfieldensis*, *georgianus*, *melanogenis*, *verrucosus*, *nivalis* and *purpurascens*)

HABITAT: Breeds in colonies on coast of main island (Grande Terre) and on offshore islands and islands in Golfe du Morbihan, on ledges 2–30 m above sea or on rocky outcrops, or among *Cotula plumosa*. Usually sheltered from prevailing winds. Sometimes nests near to rockhopper penguins (*Eudyptes chrysocome*).

COLONIES: 3–30 pairs but up to 400.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Little known; presumably breeds annually. Colonies at least partly occupied year-round. Earliest breeding recorded (presumably eggs) 11 Sept but mostly late Oct–Nov with much variation between colonies. Laying starts on av 9 Nov (24 Oct–21 Nov) and extends to at least mid-Jan. Chicks fledge mid-Jan–March. Apparently resurgence of display and nest-building may occur late March–early April; seems unusual for a seasonal cormorant.

BEHAVIOUR: Little known; probably in all essentials similar to *P. bransfieldensis* and *P. atriceps*. In a pair-interaction, ‘head-wagging’, partners face each other and sway in unison, terminating with necks pressed together, motionless. If accurate description resembles a form of mutual head-lowering found, for example, in *P. bransfieldensis*, except that it is facing instead of parallel. During male advertising head repeatedly thrown back, nape to tail.

COPULATION: (GFA)

NEST: Cone of seaweed, twigs, grass cemented with mud and guano, up to 1 m high, 33 cm in diameter; cup 20 cm across, 8 cm deep. Building may occur late March–early April; added to during incubation and material may be brought from some distance. In sheltered position, may persist and be added to in successive seasons, presumably not necessarily by same pair.

EGG/CLUTCH: (Derenne *et al.* 1976) 61.6 (58–65) × 38.8 (38–40) n = 9. Clutch 2–4, av 2.8 n = 24. Laying interval 2–3 days between eggs 1–2.

REPLACEMENT LAYING: Unproven, on comparative evidence, likely.

INCUBATION: Shared; period c29 days.

CHICK/BROOD: Hatchling black with pink gular region. Later covered with sooty brown down interspersed with tufts of grey-white. Other aspects of growth undescribed. Brood presumably 2 or 3 but no details brood reduction.

CARE OF YOUNG: Shared. Adults defend against predators (skuas, gulls, sheathbills) but lose some eggs and chicks.

Other aspects of life cycle, mortality, etc. undescribed.

Macquarie Shag *Phalacrocorax purpurascens*

PLATE 8

Carbo purpurascens Brandt, 1837, locality taken as Macquarie Island.

Sometimes placed in genus *Notocarbo*. Often considered race of imperial shag.

French: cormoran de Macquarie. German: Macquariescharbe. Spanish: cormoran de la Macquarie.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Head, hind-neck glossy black; black crest on forehead. Like Crozet, black on face extends below eye; sharply demarcated from white chin, throat and side neck; looks dark-faced. May be white filoplumes behind eye and dispersed over head, neck, back. Upperparts blackish with green sheen; thin black borders to feathers of wing-coverts and scapulars. White alar and scapular patches may be prominent, indistinct or absent; no white patch on back. Back, rump, thighs glossy blue or

purple-black. Tail black. Underparts white but some black under tail. Underwing black with white humeral line. Bill grey with horn-coloured tip to lower mandible; pair of prominent orange caruncles above base of bill. Eye-ring blue, eye dark brown, facial skin orangy with yellow spots. Legs, feet mainly pink.

ADULT F: Similar.

POST-NUPTIAL: Loses crest and white filoplumes, plumage and soft parts become dull, caruncles yellow.

JUVENILE AND IMMATURE: Brown above, white below with variably sized pale brown alar patches. Face bluish. Legs, feet pink-brown. Attains adult plumage 2nd year.

Field characters

Strongly resembles other blue-eyed shags in *atriceps* group, especially Crozet shag, but ranges do not overlap; Crozet has narrower alar bar, usually lacks white scapulars, posterior ends of caruncles point over eye whereas in Macquarie point into eye, but difficult to detect.

Measurements (see Appendix)

Voice

Colonies can be noisy; males threaten with raucous 'har' and growl; advertising males bark 'ee-oh', 'oh-arr' or 'heh-heh', first syllable during throw-back, second as head moves forward. During gaping males utter slow 'heh-heh-heh'. May call 'oh-oh-oh' when landing. May 'tick' before flight or before hop and loud 'owh' when airborne. During kink-throat loud, repetitive 'orgh-orgh-orgh'. After hop gargling 'ah-grrg'. Females hiss.

Range and status (Figure 6.134)

Restricted to Macquarie and adjacent Bishop and Clerk Islands; thought to remain close to breeding island. Brothers (1985) records 23 breeding colonies, 19 active 1975–79. May be 3–300+ breeding pairs in a colony. Total population c760 pairs including guessed 100 pairs on Bishop and Clerk. 'Rare', though not threatened.

MOVEMENTS: Local. Brothers suggests unable to progress against strong winds.

Foraging and food

In austere rocky habitat with steeply shelving shore tends to remain close in where depth is suitable for bottom-feeding. Large foraging flocks leave roosts or colonies before 10.00 hr, return c. 16.00 hr. Feed mainly along less steeply shelving W shore near kelp, among boulders, on largely bottom-dwelling fish and invertebrates. May feed singly, especially during breeding season; late March–Aug fed in groups of up to 40, diving simultaneously several times, then flying small distance and diving again. Of 47 fish regurgitated by adults and chicks, nearly half, by weight, *Paranotothenia magellanica* of mean weight 26.5 g (2.2–115.5); *Harpagifer bispinis* comprised 8.3% by weight, of mean weight 3.4 (1.0–10.0). Overall, regurgitations av 77 g (11–198); max number in single regurgitation 20 (Brothers 1985). Also at Macquarie, Kato *et al.* (1996) found *Paranotothenia magellanica* and *Harpagifer georgianus* constituted 98% wet mass.

Habitat and breeding biology

(See Fig. at end of ch. 5; Brothers 1985; extensive detail in Johnsgard (1993) under *Leucocarbo atriceps* lumps data from *bransfieldensis*, *georgianus*, *melanogenis*, *verrucosus*, *nivalis* and *purpurascens*)

HABITAT: Most breeding colonies exposed to prevailing (westerly) wind and in censuses of 1975–79 mainly on offshore or attached stacks. Two, on boulder beach, were largest. Nests close to HWM may be washed away but birds apparently not deterred from re-building on same site.

COLONIES: Nests 1–2 m apart.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually. Nuptial plumage may be acquired in June but by early Aug only 10% of nests well-built. First eggs late Sept, most laid second half Oct–first half Nov but some not until mid Jan. Storms before or during egg-laying often destroy nests. Young fledge late Jan–mid Feb.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Considerable competition for nest-sites, which are retained year on year. Often erect feathers of hindneck, crown, and crest when on site.

Unusually among cormorants, may be protracted fights, jabbing, or grasping opponent's head or locking bills, even rolling on ground locked together. Eyes and head may be severely injured.

Males advertise sitting, or standing on one or both feet, silently or with di-syllabic call, first part uttered as head moves back and second on forward swing. Crown and nape touch rump at end of throwback but head does not rotate. During earlier period of pair-interaction males may 'bark' slowly and loudly whilst gaping and head-waving (threat?), females hiss. Pre-take-off, post-landing, pre-and post-hop, kink-throating and ritualized walking, 'penguin walk', same as Antarctic shag. Mutual head-lowering not seen.

COPULATION: (GFA)

NEST: Truncated cone 20–30 cm high cemented to rock, mostly of grass, not seaweed; material collected from up to 300 m. Both sexes build and refurbish.

EGG/CLUTCH: 64 (58–69) \times 40 (38–42) $n=130$; 63.6 (58.6–67.5) \times 39.5 (37–41.4) $n=30$. Over 3 seasons clutch av 2.74 (2.5–2.93). Usually 3 eggs, often 2, rarely 1. 2-egg clutches gave rise to more fledged young than did 3 eggs.

REPLACEMENT LAYING: Lost eggs replaced but not after hatching.

INCUBATION: Possibly c32–3 days; shared about equally. Change-over morning, early afternoon, late evening. Off-duty partner spent av c. 1 hour beside nest during day (Marchant and Higgins 1990). Overnight shifts c. 15 hr, daytime 8.4 hr.

CHICK/BROOD: Black hatchling has pink throat; face pink or white. Eye dark brown, lower mandible light violet but bill dark by fledging time. Develops sooty-brown down but no details of growth. No details about reduction of brood; usually more than one chick fledges, though last hatchling often dies.

CARE OF YOUNG: When small, parents change-over c. 4 times a day. Off-duty partner spent up to 2.5 hr near nest during day. Av absence c5 hr.

BEHAVIOUR OF YOUNG: Few details. Some begin to leave nests in late Jan when likely to be c. 3 months old if laid Oct. About a month before fledging some move off nest to adjacent ones but then return. Such approaches elicit strong attack.

FLEDGING: No details: period likely to be 2–3 months (main laying late Oct, some fledge late Jan).

POST-FLEDGING: Most juveniles independent of parents by mid-Feb, soon after fledging. Post-fledging feeding probably short.

BREEDING SUCCESS: Hatched from laid: 75% ($n=119$, 3 seasons). Fledged from hatched: c72%. Fledged from laid: c54% (86 chicks from 159 eggs survived until 29 Jan). Fledged per pair: Varied 1.0–1.9 (3 seasons). Predation by skuas and starvation (often last hatchling died) main causes of death. Skuas capable of taking even large chicks if these partly exposed. Some nests washed out.

FIDELITY TO COLONY, SITE, AND MATE: Strong fidelity to colony and even precise site by male (16 kept same site for 5 years compared to 8 females); bonds often retained season to season. Tendency for young birds to breed near to natal site.

AGE OF FIRST BREEDING: Usually in 4th year or later, although may hold a breeding-site as early as 2nd year in which may even breed, though late in season. First-year and unpaired birds congregate on seaward side of colony.

NON-BREEDING YEARS: No information but paired, site-holding birds may not breed (Marchant and Higgins 1990).

LONGEVITY AND MORTALITY: Can live 13+ years. After 5 breeding seasons 41.4% of females still present; 50% still occupying original nest. 56.6% males still present and only 1 changed site. Mean annual mortality females 21.3%, males 13%.

Red-legged Cormorant *Phalacrocorax gaimardi*

PLATE 8

Carbo gaimardi Lesson and Garnot, 1828, San Lorenzo.

Sometimes referred to as *Stictocarbo* and *leucocarbo*.

Other common names: red-legged shag, red-footed shag or cormorant, Gaimard's cormorant, grey cormorant.

French: cormoran de Gaimard. German: buntscharbe, rotfuss-kormoran. Spanish: cormoran chuita, chiquitoy, patillo, pato de mer, pajaro lile.

Sub-species

Atlantic populations may be racially distinct, slightly smaller than Pacific birds and with minor plumage differences.

Description

ADULT M BREEDING: A grey shag. Head, neck, back, wings, and tail dark grey with feathers of upper back, scapulars, and wing-coverts bearing broad and conspicuous sub-terminal markings of silvery grey followed by broad black tips. Silver-grey area near tail becomes larger, forming greater part of longer coverts. Ventral surface somewhat paler, though still dark, grey. Elongated white patch on each side of neck and behind the eye a scattered patch of white filoplumes. Yellow bill merges into orange at base; face orange-red. Eye green, surrounded on rim by 16 regularly spaced, pale blue spots, 10 above and 6 below eye. Legs, feet coral red.

ADULT F: Similar.

POST-NUPTIAL: White filoplumes disappear, colours of bill and face dull, upperparts less silvery.

JUVENILE AND IMMATURE: (Rasmussen 1988) Juvenile pale brown with whitish throat, partly due to scattered white plumules here and on sides of neck. Juveniles apparently highly variable,

especially on Pacific coast, ranging from very dark throughout to pale grey below with whitish throat. Those from Atlantic coast very pale. Gular skin may be orange or dark-coloured, legs, feet dull orange to reddish black. Rasmusson depicts 4 general plumage patterns of juvenile red-legged. As matures neck patches, always discernible, become more obvious, pale brown plumage darkens. Eye may pass through pale grey to adult green.

Field characters

Grey-plumaged shag with distinctive white neck patches, marbled back, orange-red face, coral-red feet. Most resembles spotted shag, with which it does not overlap. Flight characteristically low and straight with unusually rapid wing-beats (250–300 per min) because of its short wings.

Measurements (see Appendix)

Voice

Un-seabird-like, high-pitched chirping or chirruping, like songbird.

Range and status

In Murphy's (1936) time locally abundant; now causes some concern though no adequate figures available (near-threatened, Collar and Andrew 1988). Murphy emphasized continental preference, unknown from Falklands, outlying Fuegian islets and oceanic islands off Pacific coast; sub-Antarctic in affinities. W coast South America ranges from Macabi Islands (Peru) to Chiloe Island (Chile); commonest from Guanape to Chiloe. In 1983, exceptionally large flock (c. 3,000) perhaps due to effects of El Niño, Bahia de Ancud (Clarke 1988). On Atlantic coast of Patagonia, small, isolated population at 40°S 80°W near Puerta Deseada (Argentina). Gandini and Frere (1995) report 13 colonies in Argentina (1,100 breeding pairs); half at Deseada. This country's largest colony (c200 pairs) on Isla Elena, other small groups within 5–10 km, c50 pairs at Cabo Blanco, c30 pairs on Roca Olorosa (Siegel-Causey 1987).



6.140 Distribution of red-legged cormorant. (After Johnsgard 1993.)

Yorio *et al.* (1999) give highly restricted distribution and small colonies at few sites. Numbers always on quite different scale from those of guanay with which it overlaps, but may have declined markedly in recent years. In Peru may be at most 10,000 breeding birds, in Chile uncommon and declining. Principal enemy man, from whom its dispersed cliff-sites partly protect it, though 'neither law nor sentiment does'. Though eaten, Murphy, who sampled boiled nestlings, had 'no taste for more'.

MOVEMENTS: Markedly sedentary, usually dispersing but a few km from breeding locality though sometimes up to 300 km.

Foraging and food

Essentially solitary, but sometimes in flocks, diving fairly deep (Murphy 8–10 m). Diet little known; includes eels, anchovies, planktonic crustacea.

Habitat and breeding biology

(See Fig. at end of ch. 5; Murphy 1936; Siegel-Causey 1987; Johnsgard 1993)

HABITAT: Markedly discontinuous along South American coastline dictated by preference for cliffs and rocky islets with sheer faces and no ground approach. Murphy claims that none of Peruvian guano islands, all utterly bare and rocky, lacks a few pairs. Some support (or did) several hundreds on periphery in chasms, fissures, and caves and on ledges; never on top. Coker (1919), earliest exact observer of guano birds, writes: . . . 'The home of the patillo is on the bold cliffs and in the caverns, and the body colour would give effective concealment against the rocky walls except for the brighter markings of legs and neck. . . . As one approaches an apparently bare, rocky wall rising above the surf, small, bright red spots, in pairs, may be distinguished against the gray background. If low down they may easily be mistaken for starfish or the red-legged crabs left by the tide, but these are the legs and feet of the patillo'. He adds that it is never seen except singly or in pairs but Murphy notes small flocks.

COLONIES: In favoured spots may nest thickly enough (few m apart) to form a colony though usually widely dispersed or solitary.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Not known to breed successfully more than once a year though extended laying season may imply some deviation from strictly annual cycle. Probably tends to lay mostly Oct–Feb but can nest any month and breeding seems continuous (Murphy).

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: (Resembles European and spotted shag.) Rarely moves around on land, preferring to take-off and fly rather than shuffle a few steps. Even on nest, moves by shuffling or ritualized stepping. Aggression subdued and overt fighting rare if at all, not surprising given dispersed nesting and precarious sites. Threat consists of silent, mild gape-thrust preceded or accompanied by lateral head-quivering often with retracted neck interspersed with 'worrying' nest-material.

Male's sexual advertising is a form of familiarly ubiquitous 'throwback' (GFA), here preceded by repeated head-darting—jerky movements of head back and forth in horizontal plane, accompanied by faint clicks and a slight gape, displaying red interior of mouth. After 4–5 darts lays his neck along his back, points his slightly gaping beak tailwards, holds posture a few sec and rhythmically 'kink-throats'. Significantly, as regards homology of this display, throwbacks sometimes accompanied by a single wing-flick in which folded wings flicked smartly out and back (cf. other species). A 'gaping' display, similar to advertising, is used by male when female approaches for change-over. Neck and head laid back as in throwback, with bill slightly open, and head rolled quickly from side to side, throat-clicking once with each roll. Males characteristically click and kink-throat when bringing nest-material and after copulation, holding head and neck horizontally over back of sitting bird. During pair-interactions, as also during threat, several ritualized behaviours occur as a mosaic, and clicking and kink-throating often interspersed with nest-worrying, which may be mutual. In these contexts, act of holding and arranging nest-material is displacement activity, reflecting conflicting motivations. Mutual allo-preening, particularly directed to white neck patches, often with necks intertwined, highly characteristic. May last several minutes.

At nest-site: ritualized pre-take-off posture, typically orientated away from cliff by looking over shoulder, body upright, tongue-bone lowered, followed by distinct crouch, repeatedly lowering breast and raising abdomen still with gular area depressed until bird kicks off horizontally from ledge, immediately uttering distinctive chirrup or whistle. Approaches nest from below with head and neck at 45–60° and bill gaping. Before landing throws conspicuous red feet up in front of body and vocalizes as at take-off. Immediately after landing extends neck, depresses gular area and holds this motionless for some seconds. Like other cormorants has ritualized hop, bill pointing down, neck stiffly arched, gular area depressed and wings ajar. Bird jumps upwards immediately following hop with post-landing display (above). All these signalling movements, variously combined, and at different intensities, enable partners to express subtle shifts in motivation and thus to cooperate appropriately.

COPULATION: (GFA)

NEST: Substantial, compact structure, about one-third worm tubes (c. 1.5 kg) which bind seaweed together; important on narrow ledge. Male brings material as part of pair-interactions, especially linked to copulation.

EGG/CLUTCH: 64 × 38 (n = 2, Coker 1919). Calculated weight 51g. Clutch 2–5, usually 3.

REPLACEMENT LAYING: Not recorded but likely.

INCUBATION: No details.

CHICK/BROOD: First down blackish. No details of growth and development. Despite clutch of 3 or more, brood invariably 2. Mechanism of brood reduction not recorded.

CARE OF YOUNG: No details.

BEHAVIOUR OF YOUNG: Begging of fledged young involves vigorous wing-waving and jabbing at parent's bill with shrill cries and depressed hyoid which displays gular pouch, but whether begging in cliff nests more restrained is not recorded.

FLEDGING: Presumably either waits till competent to fly from nest, or fledges before fully competent and is then fed away from nest. Juveniles fed in loose crèches below nesting cliffs (Rasmussen 1988).

POST-FLEDGING: Do not return to nesting ledge. Rasmussen (1988) observed free-flying juveniles in crèches at Punta Guapacho (Chile). Adults fed them there, rejecting some juveniles which approached and begged. Juveniles sometimes pursued adults out to sea. Period of post-fledging feeding not known. Feeding fledged young in crèches avoids difficulties of doing so on narrow ledges but what happens to those young from precipitous sites with no ground approach or sea-rocks?

BREEDING SUCCESS: No details.

OTHER ASPECTS OF LIFE CYCLE: Singularly little known.

Spotted Shag *Phalacrocorax punctatus*

PLATE 9

Pelicanus punctatus Sparrman, 1786, Queen Charlotte Sound, New Zealand.

Sometimes referred to as *Leucocarbo* or *Stictocarbo*.

Other common names: blue shag, crested shag, ocean shag, spotted cormorant, parekareka (Maori).

French: cormoran moucheté. German: tupfelkormoran, tupfelscharbe. Spanish: cormoran moteado.

Sub-species

P. p. punctatus New Zealand. Local on North Island (Hauraki Gulf, Auckland, Wellington) but common E coast South Island S to Otago.

P. p. oliveri accepted by Marchant and Higgins, considered dubious by Siegel-Causey, Stewart Island and Westland (South Island).

Description

ADULT M PRE-BREEDING: Crown, hind neck, back, belly, thighs, tail, upper foreneck black with green or blue gloss in parts. Wings, upper back, scapulars grey-brown with browner primaries; round black tips to upper wing coverts giving spotted appearance. Pale base to tail feathers. Broad white stripe from above eye down each side of neck to sides of breast, with variable amount grey. Lower foreneck, breast grey. Two conspicuous crests—forehead (upstanding), nape (thick and recurved, grading into sparser filoplumes on back of neck). During breeding, crests permanently erect. Long white filoplumes on head, neck, back, rump, thighs. Face blue or green around and below eye, to gape. Sometimes white line on throat. Eye dark brown, bill orange-brown with dark ridge, cream bar at base of lower mandible. Legs, feet orange/yellow. Brightest colouring at peak of sexual activity.

ADULT F: Similar.

POST-NUPTIAL: Crests, filoplumes lost, white stripe obscured with dark feathers, black areas of head and neck greyish, underparts can be much whiter,

eye-ring, face, gular skin less blue, bill brownish-yellow. Legs, feet pale, dull yellow.

JUVENILE AND IMMATURE: Juvenile dark grey upperparts and brown lower underparts; elsewhere paler. Feathers of upper wing-coverts tipped black. Eye brown, eye-ring pale green, facial skin, bill, legs and feet yellowish or pinkish. As it matures, much of body becomes darker with increasingly greenish gloss. Back and scapular feathers with dark spots and marginal bands, wing-coverts paler with dark tips. Grey, turning to white, develops on sides of head and on throat and sides of neck. Anterior underparts also whiten. Forehead becomes slightly crested. Facial and gular skin become yellowish, bill pinker. Legs, feet yellow.

Field characters

Slender, long-winged bird with short tail and thin bill. Rapid flight with extended neck, often in lines or Vs near surface but rising regularly. Distinguished by conspicuous black spots on grey back and scapulars, green face, orangy legs and feet, white neck-stripe.

Measurements (see Appendix)

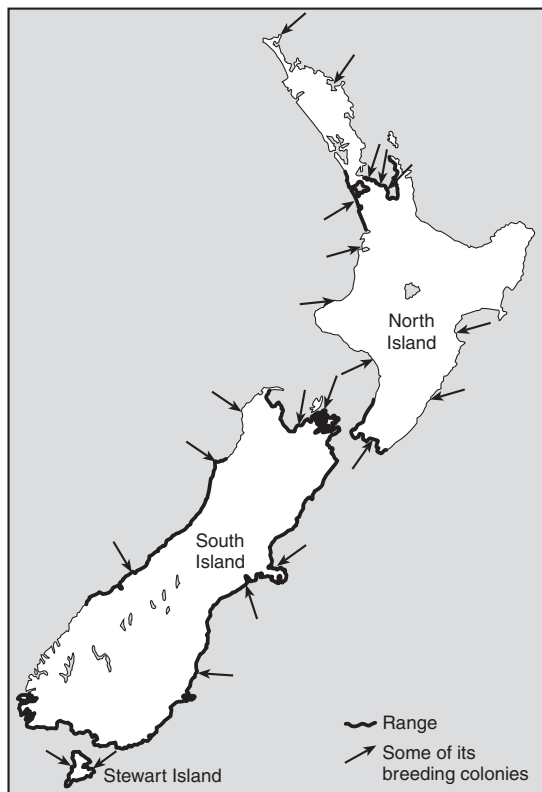
Voice

Loud grunts (male only?) at nest and loafing and roosting; male threat loud 'heugh-hergh'; also ticks 't-t-t'.

Range and status

(Marchant and Higgins 1990)

Endemic New Zealand, principally coasts of South Island, where resident and discontinuously distributed, and N of North Island and around Stewart Island where overlaps with Stewart shag. Locally common. Banks Peninsula nearly 10,000 breeding pairs 1960, >22,000 pairs 1996 (Doherty and Brager 1997). Chatham and Pitt Island birds considered to be *P. punctatus* by some (e.g. Dorst and Mougín 1979) but *P. featherstoni* by others, including Marchant and Higgins. Although locally may be systematically destroyed and disturbed,



6.141 Breeding distribution of the spotted shag. (After Marchant and Higgins 1990.)

and many colonies completely extirpated, c60,000–150,000 breeding pairs.

MOVEMENTS: Disperses outside breeding season. Most numerous shag picked up by beach patrols; highest annual total 309. Usually 100–200 found each year mostly from Canterbury and Otago beaches, peaking Aug–Sept (see Powlesland *et al.* 1993). High proportion from eastern South Island beaches does not match widespread breeding distribution around parts of North and most of South Island.

Substantial number wintering birds may congregate far from nearest breeding colony; some may remain through summer (Stonehouse 1967).

Foraging and food

Feeds singly or in groups, typically in deep water 2–16 km from shore but also in shallow estuarine water. Dives last c30 sec, preceded by smooth upward

jump. Diet inadequately known but importantly planktonic crustacea, gasteropods, small fish, including anchoveta. Feeds in association with Hector's dolphin, also near trawlers, with black-backed gulls.

Habitat and breeding biology

(See Fig. at end of ch. 5; van Tets 1965)

HABITAT: Marine shag of rocky shores, bays, inlets, and headlands though occurring also in estuaries. Strongly inclined to nest on ledges of cliffs, often precipitous.

COLONIES: Small; handful to 300–400+ (depending on definition of 'a' colony); hundreds scattered throughout range. Nests 1 m apart, usually in 'pure' groups.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually. Attends colony (other than for roosting) early July–late March. Builds Aug and lays late Aug–late Nov (Otago and Banks Peninsula, South Island), a laying period of 73–86 days depending on year, mean laying date 13–17 Oct. In Hauraki Gulf, North Island, lays late Aug–March (Marchant and Higgins).

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: (Resembles European shag more than typical cormorant.) Wide throat-gape in which head flung forward and from side-to-side, tail raised and wings akimbo. Throat bulges and male grunts loudly. Overt fighting rare and cursory.

Male advertises by wing-flicking with humeral rotation, *c.* 4 times per sec, swinging head right back, 'throwback', from retracted position, bill pointing upwards. Head position not absolutely stereotyped and may be orientated towards recipient. In backward position head rapidly darted upwards and retracted several times so that nape touches back. Van Tets (1965) categorized this as 'recognition' rather than 'advertising' but such a distinction with regard to this composite display is dubious. Not clear whether second ritualized movement (swing-pointing) is integral part of sexual advertising although clearly performed in that context. In swing-pointing neck stretched and head slowly swung right forwards from a position at base of tail to ground in front,

whilst head vibrated rapidly. Also unclear whether 'bowing', smooth arch of neck to bring bill pointing beneath lower breast, is integral component of advertising sequence or has wider context. An upright posture-plus-movement occurs as bird approaches partner; starting from horizontal, body position of 'darting' bird rises more or less upright with S shaped neck, base of which pulsates *c.* 2 times per sec. Finally gaping and pointing are used on meeting (recognition) and closely resemble elements of advertising display. Here, the several components are responding to subtle elements of context and shifts of motivation. In 'gaping' neck retracted into an S and head moved back and forth whilst in 'pointing' neck stretched forward, head and closed bill inclined upwards. Thus a range of gaping, pointing, darting, elongating, and shaking all use sinuous neck and rapid head movements.

Pre-take-off involves upwards and forwards orientation of head and neck, bill closed, throat slightly inflated, (maybe) slowly pulsating. After landing, bird may gape widely as pre-take-off but with bill forward and down, tongue bone depressed (kink throat). Otherwise, post-landing merely involves upright position. Before a hop shag may arch neck and point bill downwards, again throat distended.

COPULATION: (GFA)

NEST: Well built of interwoven seaweed and other vegetation. Outside diameter 58–79 cm, height 19–33 cm. Cup 22–41 cm, 5–16 cm deep. Material gathered from headlands (communally?) near colony and seabed. Added to during incubation but young dismantle nest which has usually disappeared before they fledge.

EGG/CLUTCH: 59.4 (55–64) × 36.8 (32.7–39.5) *n* = 48. Weight 48.8 g *n* = 12; position in clutch not specified. Clutch mostly 3 (1–4, *av* 2.7). Laid at intervals of *c*48 hours; max clutches may take 9 days to complete.

REPLACEMENT LAYING: Presumably occurs. No details.

INCUBATION: Begins after egg 2 and chicks hatch a-synchronously. Seven clutches of 2 hatched

over 4 days, 10 of 3 over 3–6 days. Shells not systematically removed; may be trampled into nest; presumably increases possibility that chicks become lacerated. Period 32 days (28–35) *n* = 13; 28–31. Change-over at least 3 times per day.

CHICK/BROOD: Hatchling *c*40 g. Dark grey, eyes closed for 2 days. Grey down appears 4–5 days, by 2 weeks down (grey above, white below) covers body but not head, which remains bare until well into week 3. Primaries erupt end week 2 and, together with secondaries, well developed by 1 month. Fastest growth occurs about a quarter of way through fledging period, reaching asymptote at 34–8 days. By fledging still slightly heavier than adult. Tarsus grows fastest, then culmen, then wing. Brood 2 or 3; *av* at fledging 1.9–2.15 for successful nests.

CARE OF YOUNG: Closely brooded until *c.* 2 weeks and fed *c.* 4 times per day.

BEHAVIOUR OF YOUNG: No details.

FLEDGING: Where topography allows, fledglings (capable of full flight?) gather on slopes below colony where (presumably) they are fed. What happens to young from narrow ledges on sheer cliffs not clear. Are first-flights fully sustainable and do they return to such sites? Fledging period *c*63 days 57–71 *n* = 34 Otago.

POST-FLEDGING: No details.

BREEDING SUCCESS: Hatched from laid: 72% (*n* = 256). Fledged from hatched: 69% (*n* = 185). Fledged from laid: 50% (*n* = 256). Fledged per successful nest: 1.9–2.2. Calculated for all nests which held eggs, figure substantially lower. Clutches of 2 eggs proportionately more successful than those of 3. Oct clutches yielded 1.69 fledglings, Sep 1.33, Nov 0.80. Figures obscure incidence of almost complete breeding failure; appear due to predation (gulls) following disturbance.

OTHER ASPECTS OF LIFE CYCLE: No substantive information on fidelity to locality, nest-site and mate, non-breeding years, and mortality rates. Likely to be comparable to European shag. Breed first at 2 years (Lalas 1983).

Little Pied Cormorant *Phalacrocorax melanoleucos*

PLATE 10

Hydrocorax melanoleucos Viellot, 1817, New South Wales.

Frequently placed in genus *Haliastur* or *Microcarbo* along with *P. pygmaeus*, *P. africanus*, *P. coronatus* and *P. niger*.

Other common names: white-throated shag; little black-and-white cormorant/shag; little cormorant/shag; frilled shag; little river shag.

French: cormoran pie. German: Australische zwergscharbe, krauselscharbe. Spanish: cormoran piquicorto.

Sub-species

P. m. melanoleucos: Australia, excluding arid inland; Tasmania; Indonesia; New Guinea; Palau; Solomon Islands; Santa Cruz Islands; New Caledonia; Campbell Island.

P. m. brevirostris: New Zealand (coast and interior) including Stewart Island.

P. m. brevicauda, endemic to Rennell Island, Solomons.

Description

ADULT M PRE-BREEDING: Upperparts, including crown, nape, back of neck glossy black, maybe with greenish-bronze sheen, with patterned appearance due to broad black borders on dark grey feathers of wing-coverts. Conspicuous white face starting above eye, broad swathe of white down side of neck. Underparts white, except for black vent and under-tail coverts. Underwing black. Small black crest on forehead, erect white frills on sides of crown. Narrow black cap; black of hind-neck expands and runs into black back. Face dark grey, gular pouch orange, bill yellow or orange, greenish towards base with brownish ridge. Inside mouth pale blue. Eye dark brown. Legs, feet black. White-throated or melanistic form, *P. m. brevirostris*, found in New Zealand, has black underparts with white confined to face, sides of neck, and variably on throat. Pied form, also assigned to *brevirostris*, much

like typical *P. m. melanoleucos* but variable amount of white on underparts. Yet another variant has smudged black and white underparts.

ADULT F: Similar.

POST-NUPTIAL: Lacks crest and frills on head, bill yellower with dark ridge, face yellow.

JUVENILE AND IMMATURE: Juvenile *P. m. melanoleucos* like non-breeding adult but duller. Black cap extends below eye from base of lower mandible; includes ear-coverts. Mottled black and white above eye. Bill black. Thighs black. *P. m. brevirostris* all-brown face and underparts. Bill black with reddish at base. Adult plumage attained late in 1st year.

Field characters

Small and tubby, black and white, long tail, noticeably short, stout bill. Many intermediate plumages exist in New Zealand, where most adults have white confined to face and throat, but size, shape, short yellow bill, and long, wedge-shaped tail distinguish it from all other Australasian cormorants. Closest congeners pied cormorant and black-faced shag but these larger with longer bills. Juveniles of white-throated form of little pied closely resemble little blacks but latter slenderer with much thinner, dark bill.

Measurements (see Appendix)**Voice**

Adults generally silent in colony but if alarmed give contagious, loud, repeated 'coo-coo-coo', when young in nest. Said to be response to aerial predators and to cause chicks to huddle and fall silent (Mathews and Fordham 1986). Vocalizes during display: repetitive 'ow-aah'; loud, clear, monosyllabic call, bill open, repeated every 1–2 sec for perhaps min or more; short, harsh 'arks' or 'uh-uh'. Reputedly a marked difference between Australian and New Zealand populations in equivalent situations (Marchant and Higgins 1990) but may be reflection of varied vocabulary and interpretation by observer.

Range and status

(See Sub-species)

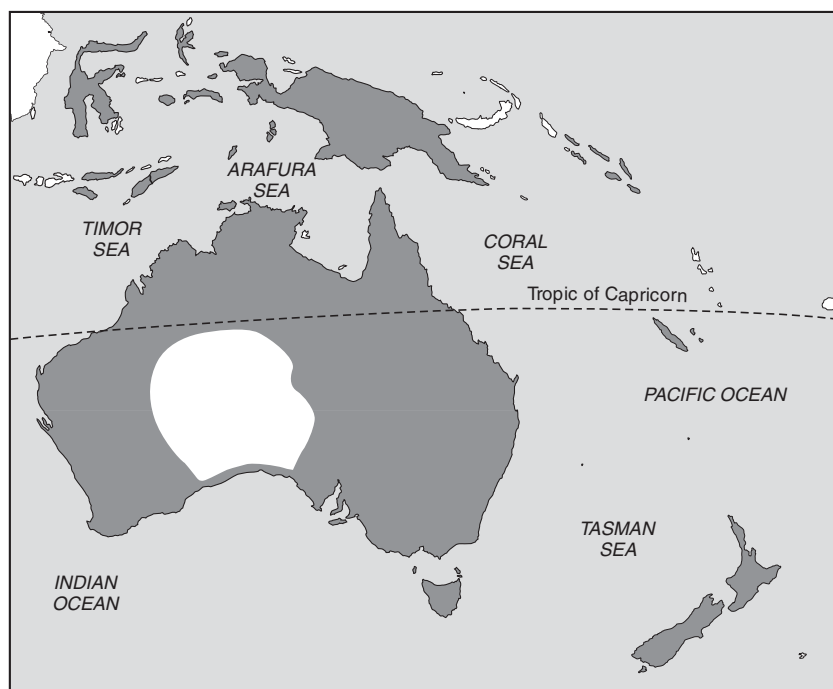
Australasia, Indonesia, New Guinea and SW Pacific, straggling to Lord Howe and Norfolk Islands. Australian population (size unknown) widespread and numerous. Alligator River (Northern Territory) flood plains 9,000 (aerial survey 1981–84, Morton *et al.* 1993). New Zealand *c.* 10,000–50,000 birds (Robertson and Bell 1984) including Stewart Island and fringing islands of North Island. In parts of Australia much natural wetland destroyed which may partly explain species' heavy use of man-made impoundments.

MOVEMENTS: After breeding, many may move from inland waters to coast or overseas. However, in New Zealand beach recoveries did not change significantly through year. Most recoveries in Otago.

Foraging and food

(Marchant and Higgins 1990)

May fly alone or in flocks. Will feed in shallow margins of large lakes and swim with only head beneath surface, presumably searching for prey. Apparently well able to feed in turbid water. Mainly solitary feeder, but fish in company with Australian white ibis which apparently may flush prey, and noted feeding in some numbers, often with little blacks (see little black for depredations on fish stocks). Described as 'cooperative' but without supporting detail to distinguish from communal. Typically dives frequently but briefly, av *c.* 16 sec or slightly more in deeper water, with rest intervals *c.* 7 sec. Unusual in feeding mostly (45–61% wet weight) on freshwater crustacea, which its strong bill can readily dismember, though also fish, particularly sluggish carp and perch and wide variety insects, sponges, amphibia. Brings large items to surface, shaking claws off crawfish



6.142 Distribution of the little pied cormorant, presumed to breed discontinuously over most of this range. (After Johnsgard 1993.)

and sometimes tossing fish before swallowing. Crustacean prey includes: shrimps (*Alpheus*, *Palaemon*, *Palaemonetes*), prawns (*Metapenaeus*), crayfish (*Cherax*, *Paranephrops*), crabs (*Amarinus*). Fish (4–18 cm) many species, including importantly *Perca fluviatilis*, *Carassius auratus*, *Apogon rupelli*, *Callogobius mucosa*, *Arenigobius bifrenatus*, *Glossogobius suppositus*. Av weight prey 24.3 g ($n=71$ birds) (Traylor *et al.* 1989).

Habitat and breeding biology

(See Fig. at end of ch. 5; Marchant and Higgins 1990)

HABITAT: Versatile; shares much of habitat with little black cormorant and both usually nest close to darters, whose nests evidently attract the cormorants (Vestjens 1975). Likes sheltered coastal waters (lagoons, bays, estuaries, including harbours), also salt pans, dune swamps. Favours large areas red river gum (*Eucalyptus comalduensis*) flooded >4 months (Briggs *et al.* 1997). Avoids exposed coasts and rarely strays beyond sight of land. Nevertheless breeds in Houtman Abrolhos (wooded Island) c70 km off coast of W Australia. Frequents natural and artefactual wetlands such as swamps, waterways of many kinds (penetrates forested creeks), lakes, ponds, reservoirs. Better able than any other species to breed in water heavily enclosed by vegetation. Aerial survey of E Australia revealed 93% of estimated population to be on artificial impoundments, nearly all on waters larger than 100 ha though this habitat cannot be typical of species. Rather reflects paucity of natural freshwater wetlands, due to drainage etc. Little piers now more widespread where forest cleared and dams built. Overall, man has greatly affected this species, changing habitat and introducing fish species now important to it.

Typically, nests moderately low in trees or in bushes or reeds in or near eutrophic waters, often among other cormorants, especially little black, but also herons, darters, spoonbills and ibises. Unlike little black, will nest on rocky surfaces.

COLONIES: Usually small, perhaps typically fewer than 100 nests but at least 300 pairs on record and

an exceptional colony of more than 1,000 nests reported from W Australia (Close *et al.* 1982). Will (rarely) breed singly. Density highly variable; often 3–4 nests per tree but sometimes many more (c. 100 in one small eucalyptus). Nests sometimes no more than 1 m apart. Unlike many cormorants, colonies appear to contain no immatures and few unattached birds. Synchronized sub-colonies occur within a colony.

FREQUENCY, TIMING, AND DURATION OF BREEDING: No evidence for breeding more than once a year. Apparently semi-continuous in Australia and perhaps to some degree opportunistic. New Zealand mainly Aug–March with most eggs laid Sept–Oct.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Breeding-site selected by male, defended by threat, repeatedly darting head, with open bill, crest raised, tail lifted and wings partly raised. Rarely makes contact. Taylor (1987) claims that, early in nesting, significant number of pairs displaced by others; overt competition for sites?

Advertising male stands erect and adopts characteristic cormorant wing-flicking posture, squatting to near-sitting position with head and bill vertical, body horizontal, tail raised, wing-tips rotated upwards. But, unlike most other cormorants, squats only briefly (c. 1 sec) before rising and closing wings. Then repeats process, hence name 'squat-thrust'. Thus instead of repeatedly wing-flicking whilst maintaining low position, achieves same effect by lowering body, raising wings only once, and then standing up again. This slows down tempo of whole display to c. 2–3 times per min compared with rapid wing-flicking of some other species. No 'throwback' or 'gargle' in this advertising and these components absent, too, in context of 'recognition'. (I consider recognition merely part of advertising display) May be that, in this species, throwback is 'throw-forward' for little pied may alternate advertising display with what has been called 'bow' or 'gape-bow', extreme forward and down movement, swinging head in vertical arc forward and

down until almost upside down on nest-site, or below feet when perching on branch. Accompanied by vocalization (guttural 'coo') which may be equivalent of gargling call in some other cormorants. Moreover (as in use of so-called gargling in context of recognition in other cormorants), 'bow' of little pied also performed on partly built nest and as pre-copulation display. As with throwback of other cormorants, restricted to early courtship and pair-bonding. Mathews and Fordham (1986) suggest this bow part of male advertising rather than just a recognition display, which is true, too, of throwback-plus-gargling of other cormorants.

Enlarged head (discoidal) seems to occur post-hop, as in other cormorants, but seems little emphasis on the 'pointing' or 'snake-necking' seen in many others, although mutual head-swaying with crest erect, bill open, and vocalization, occurs. When arriving to feed chicks, adults 'kink-throat'. During pair interactions little pied, as other cormorants, makes expressive use of forehead crest. When sitting on nest crest erect, flattened when standing. Opposite true of some other cormorants such as great and neotropic. Little pied raises crest during high-intensity threat.

COPULATION: (GFA)

NEST: Shallow, half-lined cup on stick platform. Inside 30–40 cm, c6 cm deep. Before eggs laid material brought by male. He calls repeatedly, 'uck-uck-uck' when approaching. Female accepts with neck-stretching. After laying both bring material, sitting bird accepting with neck-stretching. At nest-relief both sexes utter same 'uck' call, bill open and directed forwards, forehead crest raised and head swaying.

EGG/CLUTCH: *P. m. melanoleucos* 48 (45–52) × 32 (31–4) n = 51; 47 (45–51) × 32 (29–33) n = 29. *P. m. brevirostris* 49 (46–55) × 32 (29–34) n = 14. Weight 23 g (20–7) n = 14; 36.3 (36–7) n = 3. Looks as though first lot part-incubated. Clutch 3–5, 4 common. Occasionally 6 or even 7, though latter exceptionally high for a cormorant.

REPLACEMENT LAYING: Some lost clutches replaced but details lacking.

INCUBATION: Shared.

CHICK/BROOD: Hatchling black with red throat patch. Nestling develops woolly, dark brown down, sparse on face and throat. Well-grown young have scattered white feathers on underparts giving mottled appearance. Development apparently not recorded. No information typical brood-size; probably at least 2 or 3.

CARE OF YOUNG: Very small chicks fed on liquid dribbled into open bill; later adopt usual feeding method.

BEHAVIOUR OF YOUNG: Few details but young can swim and dive before they can fly properly. Partly feathered chicks said to scatter and take to water if disturbed though not known whether they survive. 'Doggo' response of young to alarm calls of adult seems unusual for cormorants.

FLEDGING: No details of period, manner of fledging, or post-fledging feeding.

BREEDING SUCCESS: Limited information indicates variable but fairly low success. Taylor (1987) reported 22% desertion during incubation (reason not given). In a few cases all chicks died in nest and in many others only a few chicks fledged. No pairs reared 4 young and very few reared 3. During 2 breeding seasons 43 pairs raised av 1.4 young per nest, similar to many other cormorant species.

FIDELITY TO COLONY, SITE, AND MATE: Likely to be very limited but no firm information.

AGE OF FIRST BREEDING: Acquires adult plumage very early for a cormorant—late in 1st year. At least some birds likely to breed when 2 years old.

NON-BREEDING YEARS: No information.

LONGEVITY AND MORTALITY: Not known; little-studied species.

Long-tailed Cormorant *Phalacrocorax africanus*

PLATE 10

Pelecanus africanus Gmelin, 1789, Africa.

Sometimes placed in genus *Haliastur* or in *Microcarbo*.

Other common names: reed cormorant.

French: cormoran africain, cormoran à longue queue. German: riedscharbe, reidkormoran, gelbschnabel-zwergscharbe. Spanish: cormoran Africano.

Sub-species

P. a. africanus African interior, S of Sahara.

P. a. pictilis interior of Madagascar.

Long-tailed cormorant closely related to crowned cormorant *P. coronatus*. Adapted to freshwater whereas crowned is marine.

Description

ADULT M PRE-BREEDING: Small, black cormorant with green or bronze gloss, strikingly patterned back caused by grey or silver feathers broadly tipped black. Scapulars grey-brown, also tipped black. Wings and graduated tail black. Forehead and front of crown stiff white feathers with black tips forming short (c23mm) crest. Ephemeral white filoplumes behind eyes. Eye conspicuously red, eyelids pink, facial skin anything from yellow through orange to red. Bill yellow with dusky tip and ridge, mandibles mottled reddish. Gular skin yellow. Legs, feet black.

ADULT F: Similar.

POST-NUPTIAL: Mainly dark brown above with less-contrasty wing-coverts and scapulars, which are greyish, blotched with black and edged buff. Breast pale brown becoming whitish on throat and belly; flanks and undertail remain black.

JUVENILE AND IMMATURE: Juvenile much like non-breeding adult but lacks black blotches on scapulars and wing-coverts; largely brown, dark on crown and neck, blackish on back. Broad, pale tips to tail feathers. Dirty white underparts, streaky breast. Eye

dark brown, becoming lighter (though not orange or red). Bill pinkish to yellow, with black tip. Thought within a year to be even more like non-breeding adult though may be undescribed immature stages.

Field characters

Small, dark cormorant with long, stiff tail, short yellow bill, red eye. Distinguished from crowned cormorant by long tail, relatively small body, and silvery, scaly appearance of back. Also crowned has redder bill. Brown juvenile has whitish underparts whereas crowned altogether brown except for pale throat. Agile; when alarmed takes off with ease rather than diving.

Measurements (see Appendix)

Voice

Few details. Nesting birds 'hiss' and 'cackle'. At roost bleats 'hahahaha'.

Range and status (Crawford *et al.* 1982)

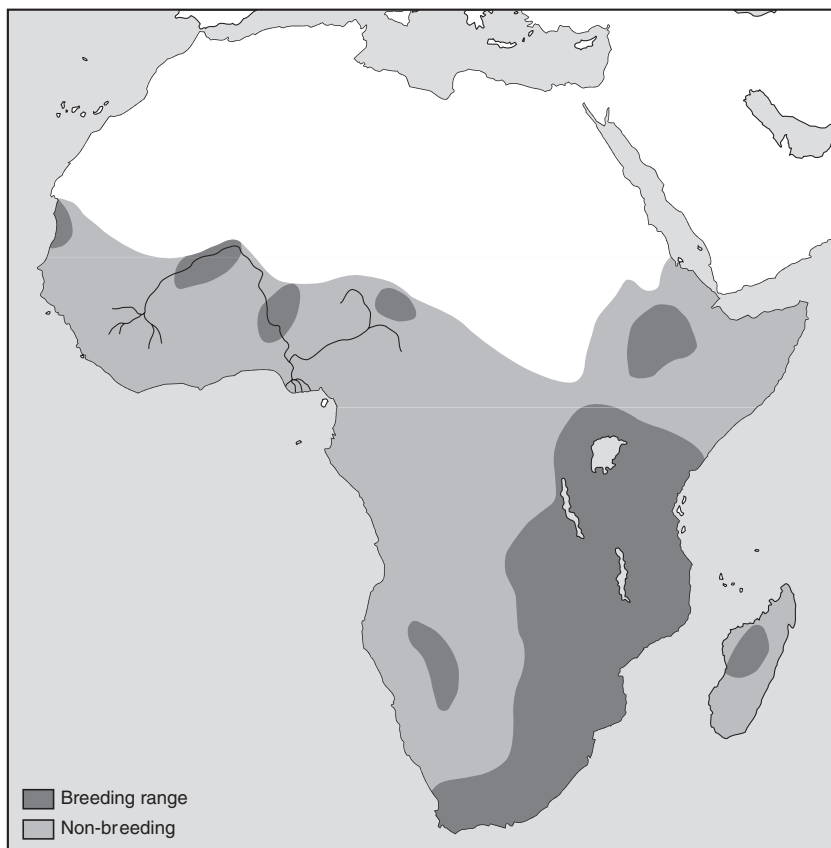
Widely distributed Africa mainly S of c. 18° N from Mauritania and Senegal to Sudan and Ethiopia, S to Cape, excluding coastal Namibia and SW Africa, where crowned cormorant occurs. Resident Sudanese Red Sea coast. Vagrant to offshore islands. Could be abundant; no estimate.

MOVEMENTS: Sedentary or dispersive, seeking opportunistic breeding. Marked migration or extensive dispersal unlikely.

Foraging and food

(Birkhead 1978; Whitfield and Blaber 1979)

Leaves roost or colony before or just after sunrise, singly or in small groups (mean 3.3 excluding singles), to favoured foraging areas perhaps at some distance. Diurnal feeder; tends to forage early morning and late afternoon, returning to roost an hour or two before sunset. Feeds singly or in loose association with other species such as pelicans. Swims low in



6.143 Distribution of the long-tailed cormorant. (After Johnsgard 1993.)

water with only head and neck showing; submerges head and then body. Feeds in shallow water (e.g. small farm dams) c2 m and within c. 100 m of shore. on small fish typically swallowed on surface. Prey varied but largely from narrow spectrum dictated by availability; includes aquatic insects, crustacea, molluscs. In Bangweulu swamp took only 16 out of 53 species found there. Important prey species: elephant fish Mormyridae, which in one area comprised 41% by weight, of its food, cichlids (70%, Lake Kariba), tilapia *Sarotherodon mossambicus*, black-band sole *Solea bleekeri*, bream *Acanthopagrus berda*. In Uganda mainly cichlids, especially *Haplochromis*. In Eastern Free State, South Africa, mean number prey items 4.0 (1–27) in 86 birds (Kopij 1996). Main prey amphibia, particularly *Rana angolensis* and *Xenopus laevis*. Fish prey mostly *Cyprinus carpio*, *Labeo umbratus* and *Barbus anoplus*. In addition, diet includes

characids, schilbeids, clariids, machokiids, anabantids, cyprinids. Most prey c7 cm (2–20) and c8 g (0.4–70); Kopij gives 2–10 cm, mostly 4–5. Av daily intake c80 g, 14–16% of body weight. Can meet daily requirements in c25% daylight hours (substantially more than many species require).

Habitat and breeding biology

(See Fig. at end of ch. 5; Olver 1984)

HABITAT: Tropical inland rivers, lakes, creeks, swamps, including mangroves, up to 1,750 m or more; also coastal lagoons, rocky coasts, inshore islands, reputedly where larger and potentially competitive crowned cormorant absent (Crawford *et al.* 1982). In some areas lives in shallow, permanent wetlands with dense growth—water-lilies, reeds etc.; often nests low over water. Inhabits

thickets of scrub or stands of trees within sedge-filled areas of water. Seems versatile in nesting habitat—trees, scrub, reeds, cliffs, rocks or sand and even in acacias far from water.

COLONIES: Usually small, tens or hundreds of pairs, often in association with other waterbirds (herons, storks, darters, ibises) but will nest singly or in 2s or 3s. Even amongst other species tends to be scattered, though sometimes nests almost touch. Komati river (Swaziland) c. 2 birds/13 km (Allan and Davies 1999).

FREQUENCY, TIMING, AND DURATION OF BREEDING: Kopij (1996) records double broods (1st laying peak mid Oct, 2nd mid-Feb), though not known whether this is typical. May breed any time of year although in seasonal areas such as southern Africa, clear spring/summer peak (Oct–Apr with 2 laying peaks, South Africa, Kopij 1996). In areas with well-defined rainy seasons nesting often associated with their onset but may begin later, or even at onset of dry season if breeding areas become sufficiently flooded and productive. Lays March–Oct (Mauritania), Jan–Feb and Sept–Dec (Senegal), June–July (Ghana), March–Sept (Ethiopia), May–June (E Kenya), Aug–Oct (W Kenya), Oct–Dec (Transvaal), Aug–Oct (Cape) (Brown *et al.* 1982). Completes breeding preliminaries rapidly as typical of opportunistic breeders.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: (Little documented; summarized Johnsgard 1993) Defends c. 1 m with aggressive forward thrust, weaving head upwards, downwards and sideways with slightly raised wings and fanned and raised tail, and raised forehead crest.

Male's sexual advertising display clearly recognizable version of wing-flicking, neck arched, bill pointing forward and up and wings flicked a little faster than once a sec. At same time, head jerked backwards and forwards and then, upon female's approach, laid back and repeatedly bobbed up and down whilst wings flicked in unison. No mention of any rotation of head. Once paired, partners smooth heads and necks over each other, touch bills and preen each other. After landing at nest, assumes 'kink-throat' and performs 'recognition'

display (bill-gaping), presumably with extended neck. Cramp and Simmons (1977) remark that interactions between partners are slight, which may relate to this species' somewhat opportunistic breeding in that pair-formation followed by rapid building and laying may occur immediately after first heavy rain. Indeed, one or both partners may still be completing moult into breeding plumage after eggs laid. May be little opportunity for gradual development of pair-bond.

COPULATION: (GFA)

NEST: Fresh, leafy twigs and other vegetation, c25 cm diameter and 2–4 cm deep. Sometimes on ground, though mean height 6.5 m (n = 192); 3.4 m (n = 200) in *Salix* spp and *Rhus lancea* (Kopij 1996). Post-copulation fetching of nest-material by male followed by nest-building, mainly by female. Once building has started constant attendance necessary to thwart pilferers. Change-over accompanied by bringing nest-material, apparently by both sexes. Nest may be completed within a week, added to throughout incubation and, desultorily, during chick-rearing.

EGG/CLUTCH: 44 (38–54) × 29 (26–42) n = 304. Weight 20.9 g n = 58. Clutch 2–6. Mean clutch 3.09 (435 nests) with regional means 2.3–3.8 (Brown *et al.* 1982). Modal clutch 4 (Kopij 1996); Olver (1984) gives av 3.6 (68 nests).

REPLACEMENT LAYING: No information.

INCUBATION: Shared. Begins with first egg. Early in incubation change-over lasts 10–20 minutes, male (if relieved) returning with nest-material. Later perfunctory (1–2 mins) with no presentation of nest-material, though still some preening (mutual?) and the ubiquitous touching of nest-material. Incubation period 23–5 days.

CHICK/BROOD: (Olver 1984) Hatchling weighs av 14.9 g n = 32. Pinkish skin blackening in first 4 days. Head pale yellow, throat red, iris pale blue. Two black lines across face. Becomes covered with black down though crown remains bare and white,

and cheeks and gular pouch red. Red skin at base of bill vivid and swollen before and during feeding. Eye pale blue. Bill, legs, feet black. Rectrices emerge c. 6 days, primaries c. 5 days reaching 10 mm at 11 days. Culmen increases from c. 5 mm on hatching to 18 mm at 17 days. Reaches mean weight 350 g (330–420) at 17 days (Kopij), max 466 g at c. 28 days, fledging at 452 g. Brood av 2.2 young reared per nest. Upper clutch-size of 6 implies some broods larger than mean, but no details of circumstances favouring such high productivity.

CARE OF YOUNG: Apparently includes regurgitating water into chick's mouth and (missed aim?) onto their backs.

BEHAVIOUR OF YOUNG: Develop rapidly and by 3 weeks can regain nest if displaced, provided nest on or near ground.

FLEDGING PERIOD: Apparently uniquely short for a cormorant; Johnsgard (1993) cites 4 weeks.

POST-FLEDGING: Apparently family parties may remain together for 1–2 months after chicks fledge, during which time young presumably fed.

BREEDING SUCCESS: Hatched from laid: 84% (n = 246, 68 nests over 2 seasons Olver 1984);

46% (Kopij 1996). Fledging from hatched: 72% (Olver); 58.5% (Kopij). Fledged from laid: 61% (Olver); 26.9% (Kopij). Fledged per successful nest: 2.2 (Olver). Three nests with clutches of 6 eggs reared most young per nest. However, mean number of young reared from clutches of 5 and 6 less than for modal 4-egg clutch, which produced 2.8 young per nest, breeding success 70%. This exceeded 3-egg clutches, indicating that commonest clutch-size (4) also most productive; may relate to age/experience of 4-egg parents. Mean fledglings per nest with eggs 0.9 n = 200 and for nests with hatchlings 1.7 n = 110 (Kopij). Most of dead nestlings found in nest; 16% fell out during winds.

FIDELITY TO COLONY, SITE, AND MATE: Likely to be low.

AGE OF FIRST BREEDING: Unknown but likely to be 2, more rarely 3.

NON-BREEDING YEARS: No information.

LONGEVITY AND MORTALITY: Rates unknown but likely to be somewhat higher than in large, less-productive marine cormorants.

Crowned Cormorant *Phalacrocorax coronatus*

PLATE 10

Graculus coronatus Wahlberg, 1855, SW Africa.

Sometimes placed in *Haliastur* or *Microcarbo*. Often treated as race of long-tailed cormorant *P. africanus* though doesn't interbreed and juvenile different. May be better treated as part of super-species.

French: cormoran couronné. German: kronenscharbe. Spanish: cormoran coronado.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Similar to long-tailed but with fewer or no white filoplumes as tuft behind eyes, longer crest. Mostly black with green sheen. Black tips scapulars; wing-coverts lack distinctly patterned appearance of long-tailed. Face orange-red, bill yellower with black spots, yellow ridge and gape. Gular skin orange-yellow, eye red. Legs, feet black.

ADULT F: Similar.

POST-NUPTIAL: Crest disappears.

JUVENILE AND IMMATURE: Juvenile brown especially on underparts, with dark brown breast and underparts, whereas juvenile long-tailed *africanus* dirty white beneath. Chin, also, darker than in *africanus*. Eye pale blue/grey. Bill blackish to horn. Immature passes through more differentiated stage in which abdomen blackens, lower breast remains dark brown with lighter flecks, upper breast, throat, and especially chin becomes lighter. Mantle feathers acquire paler edges, wings blacken. Iris reddens, bill becomes yellow.

Field characters

Smaller than *africanus* (54 against 60 cm) with shorter (though still long) tail and longer legs. Other differences as given above.

Measurements (see Appendix)

Voice

No details.

Range and status

Endemic and resident on coasts of Namibia and South Africa from Walvis Bay 22°53'S to

Aasfontein 34°46'S (Crawford *et al.* 1982). These authors cite world population *c.* 2,685 pairs at *c.* 38 breeding localities. Of 22 colonies in South Africa 7 held more than 150 breeding pairs, largest on Possession Island (Namibia) with 280 nests (in Johnsgard 1993). These figures may translate into *c.* 7,000 individuals and Crawford *et al.* do not suggest recent decline though confirm this species' vulnerability to disturbance and oiling.

MOVEMENTS: Little from breeding area (mean recovery distance juveniles 96 km, max 277 n = 7 Crawford *et al.*).

Foraging and food

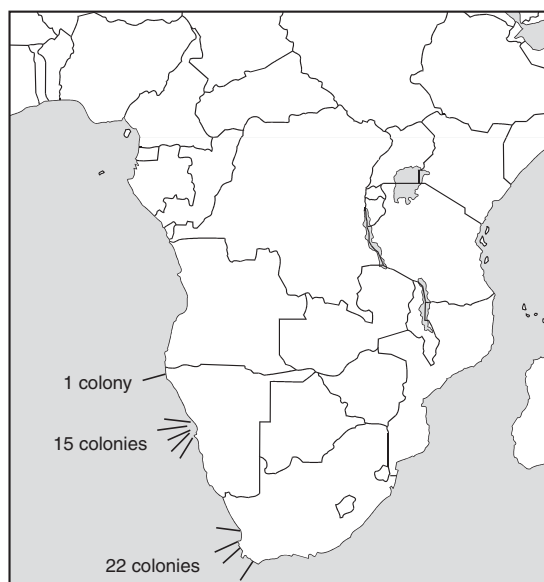
(Rand 1960; Williams and Cooper 1983)

Inshore, often on bottom in breaking water or off rocky shorelines or over kelp beds where presumably overlaps with bank cormorant. Dives short or medium duration av 23.5 sec n = 142, with 8 sec between dives. Wilson and Wilson (1988) compared foraging behaviour of 4 sympatric cormorants; found crowned cormorants dived at *c.* 45° to surface—shallower angle than that of bank and Cape cormorants. Estimated dive-speed 1.24 m per sec, speed over bottom 0.79 m per sec. Time spent on bottom depended on depth of water—the deeper the water, the more time spent. Birds foraged faster over sand than over rocks. Eats mainly fish (97% in 7 stomachs) especially klipfish (Clinidae), pipefish (Syngnathidae), blennies, mostly bottom-dwellers, but takes crustacea, cephalopods, polychaete worms, though latter possibly ingested inside other prey. Many items small (mean weight pipefish <1 g) (Williams and Cooper 1983).

Habitat and breeding biology

(See Fig. at end of ch. 5; Williams and Cooper 1983)

HABITAT: Small, agile cormorant always within 10 km of shore in cold water area of Benguela current. Virtually never inland. Overlaps with Cape and bank cormorants and geographically, though not ecologically, with long-tailed which is almost exclusively freshwater. General habits poorly known.



6.144 Breeding colonies of the crowned cormorant in Africa. (After Crawford *et al.* 1982.)

Nests on cliffs (mainland or island), flat rocks, ledges (often small) sometimes at little height, and in trees and bushes, even on walls and beaches. In all these habitats prefers sheltered rather than exposed areas, usually in company with other waterbirds. Also nests on or under guano platforms; has nested on superstructure of moored ship in Walvis Bay.

COLONIES: Usually very small (4–10 common) up to c. 150 pairs. Location may move from year to year (Williams 1978).

FREQUENCY, TIMING, AND DURATION OF BREEDING: Presumed breeds annually. Breeds throughout year, mainly late spring and summer, especially Nov–Jan. S Africa peaks spring (Aug–Dec) (Brown *et al.* 1982).

BREEDING BEHAVIOUR: Presumed similar to long-tailed.

NEST: Seaweed, sticks, detritus. Inner diameter 12 cm, cup 2–3 cm deep. Tick infested.

EGG/CLUTCH: Egg 1 of 2-egg clutches 46.4 (42.7–50.0) \times 30.7 (29.0–32.9) n = 25. Egg 2 similar. Egg 1 of 3-egg clutches 47.9 (43.3–52.0) \times 30.8 (28.8–32.7) n = 39. Egg 2 slightly smaller and egg 3 smaller still. Egg 1 of 4-egg clutches 48.3 (46.0–50.7) \times 30.5 (29.9–30.9) n = 6. Egg 2 still slightly larger than egg 2 of either 2- or 3-egg clutches, even eggs 3 and 4 not significantly smaller than eggs 1 and 2 of 2- and 3-egg clutches. Mean laying interval 2.2 days in 61 cases. Weights 22.5–24.3 g, first-laid egg heavier than subsequent, but little difference between eggs 1 and 2. Mean weight of egg from 2-egg clutch 24.05, from 3-egg clutch 24.1 and from 4-egg clutch 23.8. Even in 4-egg clutches, eggs 1 and 2 heavier than eggs 1 and 2 of 2-egg clutches. Of 1,652 clutches (some probably incomplete) 14.8% (1 egg), 39.2% (2), 44.6% (3), 1.3% (4).

REPLACEMENT LAYING: Highly likely, no details.

INCUBATION PERIOD: 23 days (mean) but 22.4 for last-laid egg of clutch. Hatching interval 1 day but

first-laid eggs presumably not fully incubated till clutch complete.

CHICK/BROOD: Hatchling 16.8 g. No weight difference between those from eggs 1 and 2, but hatchling from eggs 3 or 4 a little lighter. But feeding of first-hatched exacerbates differential by time chicks from last-laid eggs hatch. Thus chicks from egg 1 av 3.8 g heavier than those from egg 2 when latter hatched and 17.3 g than hatchling from egg 3 when it hatched. Skin pink with red patch on crown. Darkens to black within 2 days except for red patch and neighbouring skin which turns orange. Down appears days 6–7, by day 12 largely down-covered. Fine line white down develops on leading edge of underwing c. 15 days. Entire neck and crown downy at day 17. Primaries first contour feathers to develop, at day 9 and scapulars day 16. Feathers of abdomen and lower back at day 30. Although said to be capable of flight day 35, primaries still incomplete; neck, mantle and sides downy. Max weight c670 g day 30, less than lowest mean adult weight. Tarsi cease growth c20 days after hatching and feet first appendages to complete growth. Culmen still growing day 30. Little difference between weights of chicks 1 and 2 by 3 weeks. No information on mean brood-size. All chicks dying within first 20 days were last-hatched. Further comment in 'Fledging success'.

BEHAVIOUR OF YOUNG: Apparently precocious and will leave nest at c. 10 days if disturbed. By 15 days disturbed young will scramble away and join other chicks (inference is that they will return to own nest). Chick of 12 days fell into sea, swam ashore and started to climb up steep rocks to nest. By 22 days might leave nest permanently and form crèche, where will be fed. Chicks from nests in bushes or on steep slopes remained there longer than those from flatter ground.

FLEDGING: Period difficult to define. Apparently can fly by day 35 even though not fully feathered.

POST-FLEDGING: Feeding period not recorded. Probably independent 45–60 days.

BREEDING SUCCESS: Hatched from laid: 48.2% (n = 112). Included several abandoned clutches. At

27 nests where at least one egg hatched, hatching success 66.7%. Only 6.7% of 4th-laid eggs hatched. Mean number of chicks hatched in nests that hatched one or more: 2.0. Fledged from hatched: 30.4% of 23 chicks survived a min 20 days. Most chick mortality occurred in first 6 days after hatching. Last-hatched chicks of 3 and 4 broods mostly died. Apparently starvation a main cause of death, partly related to periodic inability of this small cormorant to feed close inshore during heavy seas. Under the circumstances facility to reduce brood below that which can be sustained in most favourable years is adaptive. Hatching

asynchrony and preferential feeding of strongest-begging chicks facilitates this mechanism.

FIDELITY TO COLONY, SITE, AND MATE: No information.

AGE OF FIRST BREEDING: Probably in 2nd year.

NON-BREEDING YEARS: No information.

LONGEVITY AND MORTALITY: No information.

Javanese Cormorant *Phalacrocorax niger*

PLATE 10

Hydrocoraxniger Viellot, 1817, East Indies

Sometimes placed in *Haliastur* or *Microcarbo*. Sometimes considered con-specific with pygmy cormorant *P. pygmaeus*.

Other common names: little cormorant, pygmy cormorant.

French: cormoran de Viellot. German: mohren-scharbe, mohrenzwergscharbe. Spanish: cormoran de Java.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Glossy black, tinged green. Similar to pygmy; white filoplumes on side of head from eye backwards; scattered on top of head and hind-neck. Feathers on back of head and hind-neck elongated to form a mane. Eye green, eye-ring and gular skin purplish-black. Bill dark brown to yellow-brown, more purple at base. Legs, feet dark.

ADULT F: Similar.

POST-NUPTIAL: Lacks white filoplumes, reduced crest. Generally duller with pale grey chin and throat.

JUVENILE AND IMMATURE: Juvenile largely dark brown with whitish throat and chin. Scapulars

and wing-coverts dark grey fringed with pale brown. Underparts become silver-grey before adult plumage.

Field characters

Immatures and out-of-breeding adults may be inseparable from pygmy but ranges do not overlap. Smaller than Indian cormorant, with which it does overlap, with notably smaller bill, more uniform underparts as against 'scaly' and different 'jizz'.

Measurements (see Appendix)

Voice

Highly vocal, producing uproar at roost. Deep grunts and groans and low-pitched 'ah-ah-ah' and 'kok-kok-kok'.

Range and status

Vast distribution through eastern Pakistan, India, Sri Lanka, eastward through Bangladesh, Burma and Thailand to SW China and Vietnam and Java. Probably does not breed Malay Peninsula. Common throughout much of its range: e.g. Assam, estimated population more than 15,000. Censuses in 1991 produced c36,000 birds in India, 17,000 Sri Lanka, and 5,000 Pakistan (9,000 previous year) (del Hoyo *et al.* 1992). Although still reasonably numerous, large-scale degradation of wetlands throughout its range must be greatly reducing its population.

MOVEMENTS: Basically sedentary; disperse locally into rice fields, etc. during monsoon.

Foraging and food

Although often solitary feeder, even (reputedly though unusually for a cormorant) maintaining foraging territories; quickly joins feeding flocks of Indian cormorants. Will form own foraging flocks when hunting shoals of fish. Dives often short (c. 12 sec) with rests of c5 sec but depends on where feeding. On Sri Lankan reservoir mentioned above, Winkler (1983) found that cichlids, mostly *Tilapia* and *Entroplus*, formed c50% diet, *Puntius* a further 40%. Typical feeding session may yield 8 fishes 30–70 mm. Daily intake c96 g or 20% adult weight (Winkler) seems unrealistically high though one estimate three times as high. In rice fields will feed on frogs, tadpoles, and crustacea in tiny pools.

Habitat and breeding biology

(See Fig. at end of ch. 5; Ali and Ripley 1983; Roberts 1991)

HABITAT: Lowland, freshwater species of swamps, rivers, lakes, artefactual waters. Also coastal, in estuaries and mangrove swamps. In Assam 77–85% preferred lakes and rivers to swamps and marshes. Small and inconspicuous, can live near villages where vegetation and water. Nests in bamboos, mangroves, reeds, bushes, or trees, often with other waterbirds.

COLONIES: Usually 50–60 nests at most (though larger ones doubtless exist). Nests often densely clumped, old nests may be used.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Likely to breed once a year. Extended season; laying starts around June–July in N India and Pakistan and around Nov in S India and Sri Lanka. In Indus valley of S Pakistan fresh eggs found in May. Thus with c. 4 months needed for complete cycle, may be found at some stage of breeding cycle throughout year, over species' range as a whole.

BREEDING BEHAVIOUR: No coherent account of territorial and courtship behaviour but seems latter includes typical cormorant 'pointing' with sinuous side-to-side movements of extended, forward-reaching head and neck. In advertising lays head over back; raises crest.

NEST: Small, except where annual increments enlarged it; c30 cm across base.

EGG/CLUTCH: c45 × 29. Calculated weight 20.9 g. Clutch 3–5, usually 4.

INCUBATION PERIOD: Likely to be short (less than 21 days?).

CHICK/BROOD: Down of week-old chick sooty; head and neck naked, head a startling red which, on top, persists even after down fully grown. No information on broods, growth or fledging.

BREEDING SUCCESS: No figures.

OTHER ASPECTS OF LIFE CYCLE: No details.

Pygmy Cormorant *Phalacrocorax pygmaeus*

PLATE 10

Pelecanus pygmeus (sic) Pallas, 1773, Caspian Sea.

Frequently placed in *Halietor* or *Microcarbo*. Sometimes considered conspecific with *P. niger*; Johnsgard notes separation questionable.

Other common names: little cormorant.
French: cormoran pygmée. German: zwergscharbe.
Spanish: cormoran pigmeo.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Small black or dark brown cormorant with greenish gloss especially on underparts. Scapulars and wing-coverts scaly—dark, glossy grey with black margins to feathers. Small crest on forehead, scattering of white filoplumes on

head, especially, but also on neck, back, rump, underparts. Head velvety brown-black just before breeding to deep red-brown later in season, and out of it. Eye dark brown, eye-ring, gular skin, bill black. Legs, feet dark grey/black.

ADULT F: Similar.

POST-NUPTIAL: Chin and throat become pale, patterning on upper back and wing-coverts becomes more noticeable due to narrow whitish or brown edges to feathers. Skin around gape and eyes black, tinged pink, bill mainly black-brown but yellowish with dark spots on cutting edge.

JUVENILE AND IMMATURE: Juvenile crown and neck dark brown with reddish tinge, white chin, foreneck and breast grey-brown, rest of ventral surface brownish-white with darker blotches. Flanks, under tail dark. Back scaly due to light margins to feathers and to greyish scapulars and wing coverts with dark edges. Bill yellowish. Legs, feet dark. Immature resembles out-of-breeding adult; any intermediate stages remain to be described.

Field characters

Small, short-billed, round-headed and comparatively long-(and graduated) tailed freshwater cormorant. Distinctive within its range, which is shared only by great cormorant. Differs from long-tailed by black instead of yellowish bill and in adult plumage by absence of black sub-terminal spots on scapulars and upper wing-coverts. Flies easily, often soaring; agile among emergent vegetation.

Measurements (see Appendix)

Voice

Grunts and quacks, but largely unrecorded.

Range and status

Has suffered more than most from man's activities and now occupies much reduced Palaearctic range mainly due to loss of wetland habitat, most recently in marshes of Iraq. Also much persecuted by fishermen and considered near threatened over whole geographical range and vulnerable in Europe. In

some previously favoured areas such as parts of Yugoslavia, Turkey, and Algeria has not bred for more than 100 years, though has recently returned to Hungary and Italy. Regular visitor to wetlands along Adriatic coast of Italy and recently established small breeding colony in S part of Po river delta (Volponi and Emiliani 1997). In 1994 3 pairs bred in the Reserve of Punte Alberete (NE Italy) representing the westernmost European record (Volponi and Emiliani 1995). Still breeds, or has recently bred, in Romania (c. 1,200 pairs in mid-1980s, Danube delta—now main centre in Europe, also degraded, though now winters regularly on Danube in Austria—Ranner *et al.* 1995); Albania (Lake Shkodra, c2000 pairs), Greece (Prespa), 1981, mere 80 pairs against 650 only 10 years prior; Yugoslavia; Turkey (very rare); Iraq (Euphrates); Iran 34,1991; population of former USSR c. 3,200–6,600 pairs in early 1980s mostly on Caspian sea-coast; in 1991 Azerbaijan 100 and Turkmenistan 15; breeds Ukraine (Dnestr delta); Kazakhstan to Aral Sea and its rivers though areas around Aral, in Kazakhstan and Uzbekistan now severely damaged and polluted. Size of Indian population unknown. Regularly winters in Israel where, formerly, bred. Thus pygmy cormorant, once widespread and abundant, now in retreat; even where still occurs population slumped. Current world status, at best, insufficiently known, possibly threatened.

MOVEMENTS: Winters mostly in Balkans (inland or along Adriatic coast, Aegean and Mediterranean), W Turkey, Iraq and Iran, near to breeding range. Also probably in SE Iraq (Johnsgard 1993).

Foraging and food

Feeds singly or in small groups, often in 2 sessions per day. Has somewhat un-cormorant-like habit of watching for prey from a perch, such as a reed, above water, using its tail as support. Feeds mainly on fish, including rudd *Scardinius*, roach *Esox* and small pike *Esox* up to c. 15 cm. In Danube 15 species from 130 birds recorded with max weight of 71g (Andone *et al.* 1969, cited Johnsgard 1993 'unseen'). Commonest perch (18.8%), roach (14.8%), carp (10.8%), loach (9.7%), pike (5.6%).



6.145 Breeding distribution of the pygmy cormorant (very approximate; poor and contradictory data). (After Johnsgard 1993.)

Habitat and breeding biology

(See Fig. at end of ch. 5; Nazirides and Papageorgious 1996)

HABITAT: Far inland in low-lying areas of warm, continental latitudes. Loves well-vegetated marshes, lakes, deltas, slow-flowing river systems. Eschews mountainous, dry cold regions. Favours rice-fields and other flooded areas containing scrub and trees. In winter may frequent brackish or salt water. Both solitary and gregarious. Somewhat indifferent to man. Nests often in dense vegetation; trees, shrubs, reeds, (especially) floating islets of vegetation. Usually shared with egrets, ibises, herons, spoonbills, and sometimes great cormorants.

COLONIES: 'Large' reported in marshes of Iraq and 'hundreds' cited in Cramp and Simmons (1977).

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds annually. In SE Europe and former USSR lays late April-late June or early July. Degree of synchronization within colony or area not recorded; indications that laying may be protracted could rest on replacement laying.

BREEDING BEHAVIOUR: Nothing of substance reported (but probably similar to long-tailed and Javanese).

NEST: Basket of twigs lined with grass and reeds, c25 cm diameter, with deep cup. Old nests may be

532 Flightless Cormorant *Phalacrocorax harrisi*

re-used. Material gathered from around nest, as well as fetched. At Lake Kerkini (Greece) nested 2.2–5.5 m above water.

EGG/CLUTCH: 47 (40–52) × 30 (28–33); 46.5 × 30.6
Calculated weight 23 g. Clutch 5.3 (2–8, usually 5–6).

INCUBATION: Shared; begins with 1st egg. Hatching asynchronous after 27–30 days.

CHICK/BROOD: Hatchling has black skin soon covered with dark brown down. Unfeathered head pinkish. Bill and legs bluish. Brood 3–5.

FLEDGING: Period thought to be c70 days, long for such small cormorant. But may leave nest long

before this, so precise point considered to have fledged is unclear.

POST-FLEDGING: No details.

BREEDING SUCCESS: Hatched from laid; 77% (n = 867, 165 nests, 3 years). Fledged from hatched: 89.8%; most mortality due to artificial flooding of nests.

AGE OF FIRST BREEDING: Probably first breeds when 2 years old after acquiring adult plumage towards end of 1st year.

No information on other aspects of breeding ecology.

Flightless Cormorant *Phalacrocorax harrisi*

PLATE 10

Phalacrocorax harrisi Rothschild, 1898, Narborough Island, Galapagos.

Sometimes placed in separate genus: *Nannopterum*, *Leucocarbo* or *Campsahaelius*.

Other common names: Galapagos cormorant.

French: cormoran aptine. German: Galapagoscharbe.

Spanish: cormoran mancon.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Upperparts black, or faded to brownish according to freshness, with dull greenish gloss. Underparts lighter brown. White filoplumes scattered on head and neck. Vestigial wings blackish brown, sometimes frayed. Facial skin dark, with pale dots. Gular pouch purplish. Bill, unusually long and strong, dark with horn-coloured tip. Eye small, variously described as emerald or turquoise. Legs, feet black. Body plumage soft, dense and hair-like, acting as waterproofing when outer feathers waterlogged.

ADULT F: Similar but with more numerous filoplumes on side of head and neck. Bill (lower mandible) paler than male's.

POST-NUPTIAL: Lacks filoplumes, softparts duller.

JUVENILE AND IMMATURE: Juveniles very dark (blackish-brown) with dark bill and feet, grey eye. May have a few white filoplumes on neck. Ventral surface dark.

Field characters

Only flightless cormorant. Confined to Galapagos (Isabela and Fernandina). Sexes easily separable by size (female c69% male weight) and male's heavier bill.

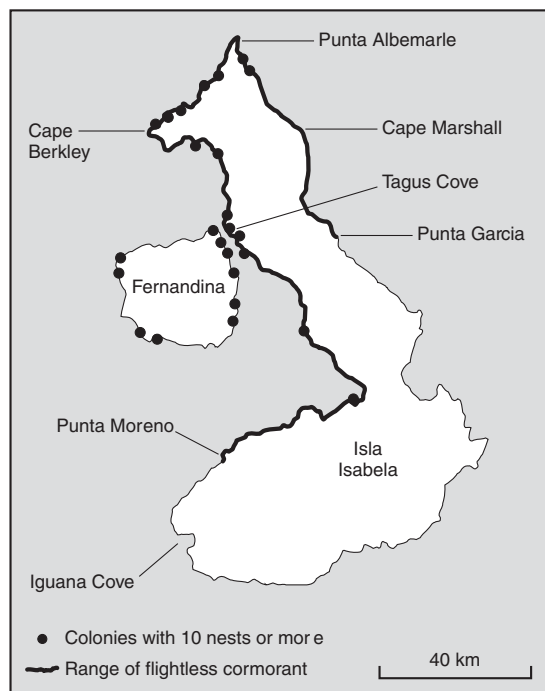
Measurements (see Appendix)

Voice

Both sexes growl or 'moo' during aquatic dance and snake-necking. 'Aaha' note produced by exhalation during sitting-gape, becoming hoarse and repetitive during aggression. Nestlings utter high-pitched 'wee-oo, wee-oo' during begging.

Range and status

First realistic figures (surveys 1970s) 700–800 pairs (Harris 1974); 1985 843 birds counted, estimated total 900–1200 birds (Valle 1986); in 1986 calculated 800–1,000 adults (Rosenberg and Harcourt



6.146 Range of the flightless cormorant (Galapagos) marked by black coastline. NB Colonies move location from year to year. (After Harris 1974.)

1987); 1992, c980 birds (Valle 1995). Restricted to 363 km of coastline of Galapagos, principally N and W coasts of Isabela and around Fernandina, two westernmost islands of archipelago. Restricted distribution probably depends on good inshore feeding (cool, rich upwelling, here Cromwell current, part of general westward flow of Humboldt). Needs suitable places to come ashore. Inevitably vulnerable but, presumably, has been so for thousands of years, though recent alteration of seabed (via fishing for sea-cucumbers) causes concern. Population may be regulated by density-dependent competition affecting, particularly, reproductive success and juvenile recruitment.

MOVEMENTS: Considered sedentary and inbred; rarely move away from own bit of coast. However, dispersal data indicate extensive gene-flow (c28 km per generation); population distributed in at least 10 relatively discrete demes or neighbourhoods, though gene-flow results in essentially homogeneous population (Valle 1995).

Foraging and food

Long ago Snodgrass and Heller (1904) noted that fed largely on octopus but also take fish—species in Snow (1966) and Harris (1979a: Table 7)—largely bottom-dwellers and up to 36 cm but also mid-water plankton feeders such as *Paranthias* and schooling fish such as *Xenistius*. Harris records single octopus 200 mm across tentacles. One regurgitate, 250 g, contained 8 fish of 4 species. Cormorants rarely seen more than 200 m from shore. Swim low on surface, often awash, and precede dive with small upward leap. Extract octopus from crevices on rocky bottom, using long, strong bills. Both sexes spend c4 hr per day foraging (same area) and catch prey about every 10–12 min (Tindle 1984). Males, it seems, dive deeper, stay longer, and take larger prey than females, suggesting that an advantageous pairing (see above) would be particularly large male with small female. In addition to atrophy of wings, body plumage has become thick and fur-like, repelling water and enabling this cormorant to remain in water for longer than would be practicable with unmodified plumage. Nevertheless retains wing-drying posture and oiling procedure of congeners, both of which probably now functionless.

Probably, flightlessness evolved because, as this cormorant became larger and heavier, advantageous in dealing with octopus, flying became unnecessary in absence of terrestrial predators. Largeness and unusually marked (for cormorant) sexual dimorphism (females only 69% male weight compared with 77–89% in other species) may have reduced competition for food (see Harris 1979a).

Habitat and breeding biology

(See Fig. at end of ch. 5; Snow 1966; Harris 1979a; Tindle 1984)

HABITAT: Requires food-rich, shallow water above rocky bottom. Great depths, just offshore in much of Galapagos, unsuitable for this cormorant. Landing places need shelter from prevailing wind and rough seas which could dash it against rocks; sloping beach of small boulders much favoured. Nests always on open, flat rock, or pebble beach.

COLONIES: Given small numbers and specialized inshore feeding not surprising that this cormorant breeds in small groups (1–20 nests but often only 2 or 3 sometimes separated by km of coast). Moves location of nesting group. Nests occasionally little more than 1 m apart but usually more dispersed.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Eggs laid in any month but 90% laid March–Oct (Tindle 1984) coincident with presence of cold, productive water. Some birds attempted to build several times a year (one male 7 times in 24 months and one female 8 in 36 months, Harris 1979a) mostly resulting from nesting failure. Intervals between successive layings partly depended on results of first. When eggs lost, mean interval 6 ± 0.74 months for males $n=30$ and 6.7 ± 0.72 months for females $n=33$. When young died, 8.5 ± 1.5 months for males $n=11$ and 7.9 ± 0.87 for females $n=16$. When juveniles survived at least 3 months, interval 13.3 ± 0.41 for males $n=11$ and 9.3 ± 1.32 for females $n=11$. Difference between sexes in latter figure probably because males feed young longer than do females. Thus during their lifetimes females breed more often than do males, suggesting either unequal sex-ratio at hatching or differential survival of young, for neither of which any evidence. All these intervals are maxima. Understandably, the more effort invested in breeding, the longer the interval between breeding attempts. In no instance did a pair produce a replacement clutch very soon after failure.

Female deserts brood partway through rearing, leaving male to complete the task. Thus she is ready to lay again sooner than she would otherwise have been and sooner than her erstwhile mate.

BREEDING STRATEGY: (Tindle 1984) Shaped by: unpredictable food supplies within and between seasons; breeding season more than long enough to allow pair to rear one brood but not long enough for two; inbred nature of colony. This cormorant's web of breeding adaptations includes frequent change of site and mate despite extreme sedentariness. Remaining in one very restricted area must facilitate intense familiarity with foraging area whilst comparatively a-seasonal breeding and

impermanent attachment to site and mate could facilitate rapid utilization of favourable feeding (and thus breeding) opportunities. Harris (1979a) suggests that in such a small and sedentary population frequent change of mate mitigates adverse effects of inbreeding by maximizing gene flow. Since females apparently realize genetic pay-off (2) greater than male's (one-and-a-bit) Tindle asked why he, rather than she, does not desert the young partway through breeding, and re-breed. Possibly, prior to desertion, she is more stressed than he, and unfit to undertake final stage of rearing juvenile single-handedly, as he does. However, apparently males suffer higher mortality. All in all, it may be (and theoretically should be) that sexes invest equally, and Tindle's analysis of their respective investments concludes that this is so.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: (Excellent detailed description Snow 1966). Uses typical cormorant threat-gape at object of hostility, with tail cocked and wings away from body, neck stretched forward, bill gaping widely and head shaken from side to side. Hyoid depressed and bird utters guttural 'a-aah'. This threat used at nest-site and at roosting and loafing places. May be brief pecking.

Unusually for a cormorant, courtship begins on water, offshore from nesting area, as mutual aquatic display or 'dance'. Posterior part of body submerged and forepart angled upwards. Swim around each other and, as they pass, incline heads towards each other and tilt them, showing underside of bill. When heads closest they growl. After one or more 'snake-neck' passes each rises far enough to flap wings and, simultaneously, raises head and bill into near-vertical position and shakes body. May spend up to an hour-and-a-half a time, more than once a day, performing in this way, gradually spending more time close to each other and eventually, perhaps, 'snake-necking' side by side. At first male showed what Snow interpreted as aggressive behaviour, swimming towards female with neck outstretched, whereupon she dived. After a time male may lead way shorewards, periodically 'snake-necking', whilst female follows without this posture. Occasionally male dives, immediately followed by

female and both swim underwater, maintaining their distance. After landing male may display further, performing a 'throwback' and 'bow' whilst female snake-necks in water or joins him ashore. They might land at several different places, usually where already nesting cormorants. Snake-neck used, also, on land. Body held upright, feathers flattened and wings closed. Feathers of head and neck erected, enlarging head. It is angled, depending on orientation of display, but mid-neck always pulled backwards giving snake-like appearance, and bird growls with closed bill. During growl air exhaled producing dent in upper breast. Hyoid may be lowered. Birds snake-necking close together incline heads towards each other, tilt top of head away and growl in unison. At high intensity and just as on water, partners stretch upwards and wing-flap. Snow thinks this wing movement, which she calls 'flutter-up', is homologous with ritualized hop of many other cormorants but that actual hop omitted because of bird's weight. Besides occurrence during courtship, snake-necking used as 'recognition' display when well-established courting pairs meet after moderately long separation but not, it seems, once there are eggs or young. This is consistent with similar use of 'throwback' in other cormorants. Snake-necking thus conspicuous and common element in this cormorant's display; given by a bird approaching or leaving site even if partner absent. Males collecting seaweed often perform incomplete snake-neck with growl. Growl so characteristic of courtship that subdued one may be uttered without snake-neck, even when bird resting (or sleeping!) alone on site. In such a case, stimulus fundamentally internal. When prospecting for nest-site either sex may lead, snake-necking at intervals.

'Throwback' performed only by male and noteworthy because reduced in amplitude and complexity and seldom used, its place as advertising behaviour having been taken over by aquatic display. It is brief, backward throw of head to mid-back, bill vertical. Tail un-fanned and wings motionless and folded. Usually followed by 'bow'. Nevertheless still, functionally, an 'invitation' for female to approach, usually in early stages of pair-formation and when male on nest-site. Presumably, as phylogenetically ancient display, may be older

than aquatic display, which may have evolved along with flightlessness. Once pair bonded it stops and even in earliest stages throwback may be omitted and bow and snake-neck used to invite female. In bow, bill pressed against neck and upper breast and accompanied by a repetitive call, 'oncha, oncha'. Hyoid depressed and in-and-out breathing exaggerated enough to make upper breast palpitate. Head and neck feathers ruffed. At first it is male display, performed when female reaches his side, but later both sexes do it, both standing and sitting. In latter case bird may hold nest-material or dig bill into rim of nest. When female 'sit-bows' she cocks her tail and raises lower back in soliciting position. Bowing becomes infrequent during incubation and chick-rearing. Seemingly, mates do not preen each other although Snow suggests that vestigial allo-preening manifested by female resting bill tip in male's nape feathers during (or after?) his bow, based on observation that when male European shag bows female preens back of his head and neck, failure to do so resulting in break-down of courtship sequence and in aggression from male.

COPULATION: (GFA)

NEST: Approx 40–50 cm across base, mostly seaweed and detritus on bare lava. Male collects material and may swim underwater with it. Building, mainly by female, may take 4 weeks. Lateral head movements which in other cormorants interweave sticks seem functionless in flightless cormorant, because only nest-material wet seaweed.

EGG/CLUTCH: $67.4 \pm 0.32 \times 42.1 \pm 0.12$. Fresh weight: egg 1 71 g, egg 2 67.5; each egg c. 2.6% female. Calculated weight 67.4. Clutch usually 3 $n = 83$; 2 $n = 19$; 1 $n = 5$ and 4 $n = 2$. Eggs laid 10–40 days after nest built; incubated from laying of egg 1.

REPLACEMENT LAYING: Possibly occurs. Tindle says 'even if not re-laying immediately' which implies may do so. Harris (1979a) found none.

INCUBATION: Shared. 'In' bird does sitting-gape with kink-throat when partner arrives. Gapes in upward direction with mandibles open to c40°

accompanied by slight lateral head-shake and 'aagh' call. Sitting-gape closely tied to being on nest and stops as soon as change-over effected. Incubation period 33–7 days $n=6$ first laid to first hatched. Hatch a-synchronously. Shifts vary, probably 2–5 per bird per day though in some change-over occurred only once in day (Snow).

CHICK/BROOD: Hatchling pinkish-grey with pale pink gular pouch. Eyes open at least as early as day 3, down appears about day 9 first on back then underparts and last on neck. Down-covered except on head by day 14. Gular pouch becomes mottled black and is uniformly dark at fledging. Mean brood at hatching 1.7 (42 nests with 2, 39 with 1, 10 with 3). Later usually only 1; younger soon starves but occasional broods of 2 survive; younger chick may survive if older fails.

CARE OF YOUNG: Chicks shaded in hot weather and attended by one parent even when large (40 days). Adult returning with food usually withholds it for an hour or two even though chick begs. Snow suggests anti-theft behaviour against frigatebirds.

BEHAVIOUR OF YOUNG: Even tiny chicks beg with distended gular pouch and 'wee-oo' vocalization. Agility improves rapidly and by day 12 chick can climb back into nest up 25° slope, though unable to do so a day or two earlier. Uses bill as prop and lever with wings held out. Wing-exercising by *c.* 5 weeks. Threat-gaping with shrill 'wee-aa' when *c.* 3 weeks, interspersed with handling nest-material.

FLEDGING: Young take to water at *c.* 2 months.

POST-FLEDGING: Continue to be fed for several months after taking to water, even when known to be catching food for themselves. Harris (1979a) noted feeds given by male parents to juveniles aged 5 and 9 months, and by females or sex-unknown adults to young aged 4 months. Males feed juveniles for longer than do females. Latter may start new clutch with different male whilst previous male still tending juvenile (opposite to strategy found in magnificent frigatebirds). Tindle (1984) states that females desert young of 70–90 days and

these fed for 5–9 months by male alone. This period, longest for any phalacrocoracid, may reflect specialized feeding technique. Juvenile swims to meet incoming parent, food-begging by waving head in an arc, calling 'wee-oo' and beating wings. Partly dependent juveniles apparently do not join loafing, non-breeding adults.

BREEDING SUCCESS: Hatched from laid: 62% (1970–75 expressed as percentage of clutches that produced one or more young). Although usual clutch 3, only 2 chicks hatch; Snow suggests 3rd egg unfertilized and Harris adds that in many clutches all infertile. Fledged from hatched: 82%. Fledged from laid: 51% (Harris 1979a) but varies considerably between years, seemingly correlated with sea-temperature. This controls food, which triggers breeding. Groups of nests may be abandoned almost synchronously. Each clutch produced 0.51 juveniles (this need not mean independent juveniles). Relatively few clutches laid Nov–March. Significantly less successful than those laid at other times, mainly due to high proportion which failed completely. Very few pairs rear 2 chicks; usually younger starves although Harris records that of 70 juveniles where brood-size at fledging known, 18 came from broods of two. One chick commonly lost soon after hatching, though nobody has suggested siblicide. In 1972 breeding season, when sea temperatures unusually high, only 0.14 juveniles per pair produced compared with av 0.6 in other years. Moreover only 25% of juveniles survived the first 3 months after fledging compared with av 77% in other seasons. By contrast, adult mortality not noticeably higher than normal, which supports proposition that adult tropical seabirds ensure own survival by abandoning eggs or young in difficult times. Snow recorded 9 nests with eggs or young in June but only a single juvenile at time of her second visit.

FIDELITY TO COLONY, SITE, AND MATE: See earlier comments on distribution and unequal breeding frequency of male and female.

AGE OF FIRST BREEDING: Mean 30 (23–38) months for males $n=6$ and 29.5 (17–50) for females $n=10$. However, 18 month-old built a nest though no

eggs ensued. Circumstantial evidence suggests breeding further deferred if year in which would have bred, poor. Nevertheless uniquely early breeding for a seabird with such long post-fledging dependency.

NON-BREEDING YEARS: See earlier for relationship between breeding and food.

LONGEVITY AND MORTALITY: Adults: between 1970 and 1975 Harris recorded an annual mortality of females of 8.6% and males 17.6%. However, in one year every male (20 in all) survived from previous

year and 91% of 74 females did so. Re-catching birds in 1970 and 1975, ringed in 1962, indicated minimum annual survival rate (sexes not differentiated) of 87% over 13-year period. Tindle (1984) gives annual adult mortality of both sexes as 15%. Pre-breeding: 30 of 53 juveniles known to have survived 12 months after going to sea, a minimum survival of 56.6%. Survival of birds that have reached one year old similar to that of adults.

From these figures it may be estimated that adults of this cormorant have an life-expectancy probably exceeding 15 years and, in individual cases, considerably more.

Anhinga and Darter

Anhinga *Anhinga anhinga*

PLATE 10

Plotus anhinga Linnaeus, 1766, Rio Tapajos, Para, Brazil.

Common names: American darter, suckerbird, black darter, black-bellied darter.

French: anhinga d'Amerique. German: Amerikanischer schlangenhalsvogel. Spanish: anhinga Americana.

Sub-species

A. a. leucogaster (Viellot 1816) USA—North Carolina to Texas, Central America, Cuba.

A. a. anhinga (Linnaeus 1766) South America from Colombia to Ecuador, east of Andes to northern Argentina, Trinidad and Tobago.

Description

ADULT M PRE-BREEDING: Black body plumage; green-glossed, head and neck browner due to elongated, transitory brownish white filoplumes on hindneck and head, bordering central mane. Elongated scapulars, wing-coverts and longest proximal secondaries silvery white; other wing feathers black; alulars unusually long. Longest wing-covert feathers corrugated. All 14 tail feathers black (mid-pair corrugated with c. 30 transverse flutings) becoming browner towards tip and tipped with brownish white. Bill nondescript dusky greenish on upper mandible, more yellow lower mandible; early in courtship becomes orange red. Iris red; orbital ring, lores, face yellow

green early in breeding season, turning bluish, finally emerald or turquoise at peak of courtship. Gular skin yellow or pink early in season turning black at peak. Gape black. Legs, feet dusky olive with yellow on webs.

ADULT F: Head, back of neck brown, feathers fringed whitish or rufous. Sides of head, throat and upper breast pale buff. Upper back black, feathers with brown margins and pale centres. Rest of upperparts similar to M. Belly and lower breast black. Bill drabber than M but sometimes bright yellow or orange with bright blue base. Iris paler than M, from pale red to darker red or yellow. Orbital ring, lores, face bright bluish during peak courtship. Gular skin orange becoming black at peak courtship. Legs, feet orange brown. Nail of middle toe flanged and serrated.

POST-NUPTIAL: Lack filoplumes, M lacks mane, pale tips to tail abrade, flutings less conspicuous. Colours of soft parts duller, orbital ring and lores drab, bill darker, gular skin olive in M, yellowish in F. Legs, feet dark olive with paler webs.

JUVENILE AND IMMATURE: Sexes similar buff head, neck, upper breast; brownish white underparts. Back feathers dusky with lighter borders; wings, tail darkish with silvery markings. Even at this stage, rudimentary white stripes down middle of scapulars and coverts though transverse flutings

of inner secondaries and central tail feathers barely apparent. Definitive plumage reached in 2 years.

Field characters

Large size, long thin neck. Small head, thin straight bill and long tail unmistakable in marking it out from large cormorants. No overlap in distribution with darter.

Measurements (see Appendix)

Voice (GFA)

Range and status (Figure 6.147 and GFA)

Little known about numbers over most of range—largely in South America. In North America population *c.* 4,500 birds, mostly in Louisiana and Florida (Johnsgard 1993).

MOVEMENTS: Largely resident but may move hundreds of km from colony.



6.147 Distribution of the anhinga. (After Johnsgard 1993.)

Foraging and food (GFA)

Prey (fish, reptiles, amphibia and invertebrates, including crustacea and insects) generally slow-moving, mid-water or benthic, generally narrow-bodied (Owre 1967). Largest recorded 13.2 cm × 4.5 cm. Fish (mainly 4 families: Cyprinodontidae, Poeciliidae, Centrarchidae, Percidae) includes pickerel *Esox*, suckers *Cotostomus*, mullet (*Mugil*), sunfish *Lepomis*, mojarrita *Eucinostomus*, gizzard shad *Dorosoma*, bream, catfish (Ameiuridae).

Habitat and breeding biology

(See Fig. at end of ch. 5; Palmer 1962; Owre 1967—mainly feeding; Johnsgard 1993; no recent details)

HABITAT: Prefers largely shallow freshwater, such as flooded areas (permanent or at least four months), not too muddy and with emergent vegetation, such as Red Gum river (W Australia). They use living nest trees, often choosing comparatively high sites on the outer edges. In N America favours cypress swamps (93% breeding pairs) and uses mangrove swamps and tidal estuaries. In southern USA 90% favoured fresh water, 9% brackish but none fed in salt water (Portnoy 1977).

COLONIES: In Argentina anhinga colonies contained around 400 nests (Parera and Bosso 1996). In N America they were 1–3 birds (44), 51–100 (11), 101–200 (4), 201–500 (1), 501–1,000 (2) (Johnsgard 1993). In Swaziland (Africa) nesting density was 1.3 birds per 13 km (Allan and Davis 1999).

FREQUENCY, TIMING, AND DURATION OF BREEDING: Generally assumed to breed once per year. In Florida, peak of laying during late winter and spring (mid March–end April) although may breed at any time of year. On W coast of Mexico laying peaked mid-July (rainy season).

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Apparently lacks ritualized site-ownership display but reacts to potential or actual intrusion by threat and occasionally overt grappling.

In presence of (presumably potentially receptive) female, though occasionally without one, males advertise by wing-waving, variously described as

'wing-flicking', 'wing-waving' or 'wing-fluttering'. Movement begins with sitting bird, neck stretched, bill and tail pointing upwards, moving both wings, in folded position, up and down in concert. Then wings move alternately c. 2 times per sec and body begins to sway. Tail depressed, head and neck feathers erected (Johnsgard 1993). Presumably (though not stated) wing-waving followed by 'snap-bow', precisely comparable to great cormorant's 'wing-flick' followed by 'throwback' as single composite display. In anhinga's snap-bow body horizontal, tail spread and raised, then bill raised vertically and thrown back (as in cormorant's 'throwback') before being sharply extended forward with bill pointing down, at which point tail passes beyond vertical. In this posture bird lowers head below foot level and moves it slowly from side to side, meantime waving (or flicking) its wings alternately. May hold this 1 min or more. During snap-bow anhinga vocalizes, just as cormorant does after throwback. After forward bow anhinga may snap mandibles or seize and shake nearby twig, not as a functionally discrete display but probably redirected aggression as commonly occurs in cormorant and sulid pair interactions.

On-site bird, when joined by mate, may seize and shake nearby twig (redirected aggression?) or 'forward-point', or pair may make bill contact or extend necks across each other's in typical cormorant fashion, or 'bow'. Also mutual preen.

COPULATION: (GFA)

NEST: In Mexico av 2.45 m above water and 80% sited between trunk and side branches. All had exposed perches nearby. Made of twigs, at first leafy, and may be so loose eggs can be seen from below, or may be substantial basket persisting from year to year.

EGG/CLUTCH: Pale bluish-green, overlaid with thin limy covering, sometimes with dark brown spots. Longish oval. Measures $52.53 \pm 2.24 \times 34.89 \pm 1.26$ n = 20 (all from different clutches in Florida or Texas). Weight 35.2 g or 2.89% female's weight. Mean clutch 3.89 (2–5) n = 16 (Mexico); 3.8 (2–5) n = 29 (Arkansas). Eggs laid daily or one in 2 or 3 days. Clutch of 4 only 11.5% female weight.

REPLACEMENT LAYING: No details.

INCUBATION: (GFA) Approx 28 days, mean 27.8 for 1st-laid eggs n = 14. Hatching at similar intervals to laying even though incubation begins with first egg. Shifts, M av 2.67 hr, F 1.56 hr, though either may incubate for at least 8 hr.

CHICK/BROOD: Hatchling naked with yellowish skin, pale pink head and yellowish legs and feet. Bill and eye dark and gular pouch orange. In 1–2 days uniformly covered with pale buff down, becoming white on sides, rump, and belly at c. 10 days. At 2–3 weeks back and hind neck covered with white and buff down. Dark scapulars and wing feathers then erupt. At 7 weeks can swim, dive and fly 200 m, a feat quite unequalled by any other pelecaniform. Brood av 3.

CARE OF YOUNG: Chicks brooded continuously for 10–12 days, then may be left unbrooded. Harriott (1970) says female alone cares for young after first month. Parents feed young by incomplete regurgitation using, for tiny chicks, a method found also in pelicans, sulids, and cormorants, where adult rests angled upper mandible upside down on nest, allowing food to run down trough to tip from which taken by chick. Older chicks take food from adult's throat in usual way. During first 2–3 days may be fed 6–9 times per day, at 2 weeks 2 times per day and at 5 weeks once per day. Darters (and presumably anhingas) bring water and pour it into chick's widely opened bill. In hot weather said to wet plumage and shake it over chicks. Once young can fly properly further feeding by adults must be limited since young disperse soon afterwards.

BEHAVIOUR OF YOUNG: Reputedly, anhingas can move from nest at 10 days, seems extraordinary; Johnsgard (1993) says they can 'take a few steps' but perhaps in response to disturbance. By week 3 chicks may move onto branches which they share amicably with neighbouring chicks. By week 4 they exercise their wings, hop amongst branches and can swim (and presumably regain the nesting tree). By weeks 5–6 they tend to drop into the

water when disturbed and can dive. After week 7 they can fly up to 1.5 km; unprecedented in any other pelecaniform. They disperse soon after they can fly properly.

FLEDGING: Period 56–60 days.

POST-FLEDGING: Not known to be fed by parents after about 60 days.

BREEDING SUCCESS: Hatched from laid: *c.* 81% (*n* = 77 in 21 nests); 74% (*n* = 10 nests). Fledged

from hatched: *c.* 73% (*n* = 19). Fledged from laid: no figures.

FIDELITY TO COLONY, SITE, AND MATE: (GFA) Comparative information from cormorants suggests unlikely to remain faithful for more than 2 successive seasons.

AGE OF FIRST BREEDING: Palmer (1962) says not less than 2 years.

NON-BREEDING AND MORTALITY: No information.

Darter *Anhinga melanogaster*

PLATE 10

Anhinga melanogaster Pennant, 1769, Ceylon and Java.

Common names: African darter, Australian darter, oriental darter, Indian darter, needle-beak shag, snake bird.

French: anHINGA roux. German: schlangenhalsvogel. Spanish: anHINGA comun.

Sub-species

Sometimes treated as 3 distinct species.

A. m. melanogaster Pennant 1769 India to Philippines and Sulawesi. [PLATE 10]

A. m. rufa Daudin 1802 Africa, S of Sahara, Middle East. Madagascan and Iraqi populations sometimes distinguished as *vulsini* and *chantrei* respectively. [PLATE 10]

A. m. novaehollandiae Gould 1847 New Guinea and Australia. [PLATE 10]

Description

ADULT M PRE-BREEDING: *A. m. rufa*—crown, nape, and hindneck dark blackish-brown. Side neck and foreneck chestnut with longitudinal white stripe, edged black from cheek and down neck and bearing inconspicuous filoplumes. Chin and throat buff. Mantle, back, rump, upper tail coverts and all the underparts black with oil green gloss or brown. Primaries, secondaries, and tail black. Scapulars, tertials, and wing-coverts black with conspicuous white stripe down centre of feathers. Scapulars

acute and elongated (least in *novaehollandiae*, most in *melanogaster*). Secondary coverts reddish brown in *rufa*, pale brown in *novaehollandiae* or silvery in *melanogaster*. Underwing black. Central pair tail feathers with *c.* 30 transverse corrugations, longest wing coverts similarly fluted. Bill greenish horn or yellowish. Face brownish or more yellow; gular skin cream to greenish black. Iris yellow; orbital ring yellow or brown. Legs, feet grey or brown (vary with season and area).

ADULT F: All forms, but particularly *novaehollandiae*, sexually dimorphic. Differs from M in having head and midneck reddish-brown instead of blackish, bordered by whitish band. Black foreneck and upper breast, bordered by rufous band. White stripes on scapulars more conspicuous than in M. Underparts whitish in *novaehollandiae* but blackish in other two. Legs, feet pale brown/yellow.

POST-NUPTIAL: Head, neck, mantle browner, white neck streak lacking black border and sometimes separated from hindneck by pinkish-buff area. Soft parts duller.

JUVENILE AND IMMATURE: Grey crown and hindneck, buff on sides of head and on neck (lacks white streak). Upperparts dark brownish. Wing coverts edged pale brown. Underparts mostly pale buff with dark brown flanks and thighs. Black tail feathers lack ribbing. Bill grey-green; gular pale yellow, pink or

orange. Iris brown with yellowish and then whitish towards centre; orbital ring green. Legs and feet brown. Definitive plumage attained at 2–3 years.

Field characters

Large size, long thin neck, small head, thin straight bill and long tail unmistakable in marking it out from Cape cormorant. No overlap in distribution with anhinga.

Measurements (see Appendix)

Voice (GFA)

Range and status (Figure 6.148)

Rufa: Widely distributed and common in sub-Saharan Africa S to Cape of Good Hope. Resident Madagascar and (until recently) on Lake Antioch and Hula, and Tigris–Euphrates delta in Iraq.

Melanogaster: Resident India, Pakistan and throughout most of Far East. Formerly also Malaysia and Turkey. Resident Sri Lanka.

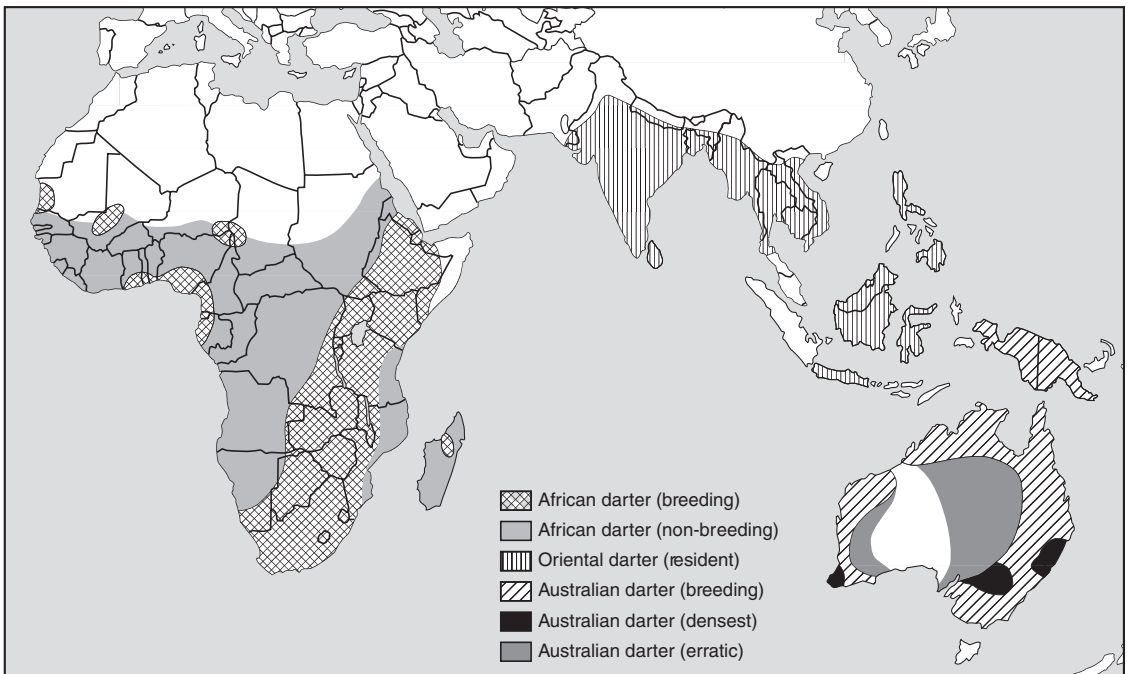
Novaehollandiae: Resident coastal Australia and New Guinea lowlands.

Total numbers of all these races unknown, but, e.g. Alligator river region (Northern Territory, Australia) held estimated peak 2,000 (1981–84) (Morton *et al.* 1993).

MOVEMENTS: Largely resident but may move hundreds of km from breeding area.

Foraging and food (GFA)

On lake Kariba (Zimbabwe) cichlids formed main prey, particularly *Haplochromis*, *Pseudocrenilabrus* and *Tilapia* (Birkhead 1978). Mean prey length 8 cm (2.2–16.5) and mean weight of individual items 9.89 (0.5–73.1). In Uganda, by contrast, Cott (1961) found few *Tilapia* and not *Pseudocrenilabrus*. In W Bengal Mukherjee (1969) found that oriental darter took mainly fish of 50–150 mm together with insects (8.4%), snakes (7.4%) and a few tadpoles and crustacea. In Australian they take many introduced fish such as perch *Perca* and goldfish *Carassius*. Vestjens (1975) found prey av 130 mm (90–198). Dostine and Morton (1989) found that in N Australia darters fed more on smaller, native fish (9 sp, 7 families, mainly



6.148 Distribution of the darter. (After Johnsgard 1993.)

catfish). Prey measured 27–161 mm. Caught many benthic rather than agile midwater ones.

Habitat and general biology

(See Fig. at end of ch. 5; mainly—Australian darter—Vestjens 1975; Cramp and Simmons 1977; Johnsgard 1993)

HABITAT: Darters prefer interior wetlands, especially lakes and sluggish rivers but also estuaries and coastal waters with edge vegetation.

COLONIES: Up to 5 nests per tree, occasionally neighbouring nests almost touching. In Africa, colonies consist of a few up to several thousand pairs, in trees or reed-beds usually 1–6 m above the water (Brown *et al.* 1982) but darters may nest solitarily.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Supposed double-brooding in Ghana (Bowen *et al.* 1962) needs confirmation; comparable bimodal pattern in Australia did not involve double-brooding. Seasons variable and extended. In Africa may breed year-round or seasonally. Mostly nests at end of rainy season or during dry season (details Brown *et al.* 1982). In Australia breeding seems irregular, perhaps in relation to food availability. N India and Pakistan breeds June–Dec; S India Nov–Feb; Sri Lanka Jan–March (summarized Johnsgard 1993). Anhingids have shortest complete cycle of any peleciform.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Potential intruder dispelled by site-owning male who hops and flies towards it, calling. Bill snapping and stabbing bouts to head and neck may ensue. Female–female encounters rare and generally do not include stabbing.

Male, often on site with nest-material or even old nest, or on nearby branch, ‘advertises’ to female who may be prospecting in flight or have landed nearby. Male points towards female with stretched neck and bill and tail at about 80°. Then ‘wing-waves’, alternating wings at irregular speed, faster as female approaches. Bill downward at c. 45° and may grasp and shake twig. If female approaches, male thrusts head forward and down (the ‘snap-bow’)

with closed bill (see anhinga), meanwhile uttering one or two explosive ‘chaahs’. This composite display very similar to anhinga. As female approaches she makes horizontal back-and-forwards head movements, bill open or closed, calling softly. Male responds with calls and ‘pointing’, head waving slowly from side to side or motionless and directed upwards, tail slightly raised. Partners may pass necks over each other’s (‘neck rubbing’). Johnsgard says that at this stage male and female may perform modified version of snap-bowing, raising and vibrating folded wings and snapping bill. Male may eventually depart and fly round. Female may move onto nest, vocalizing. Male returns, uttering 3–15 loud calls (rolling ‘kah’) whilst flying in. Female ‘points’ as male moves onto nest. Vocalizations, attributed to context of ‘greeting’ at nest, include for both sexes repeated ‘kek’ notes (= ‘clicks’?), sequence 2–4 sec and speeding up towards end.

Other displays performed in so-called ‘recognition’ context (partners meeting on site): modified version of snap-bowing, which terminates after egg-laying, ‘gaping’ and ‘wing-lifting’. In gaping female shakes head vertically and horizontally with open bill; male may nibble her bill and insert his into hers (also seen in anhingas). Observed only prior to copulation. In wing-lifting, ‘out’ bird, approaching nest, ‘kink-throats’ and calls with ratchet vocalization. ‘In’ bird makes S-shaped neck and lifts wings simultaneously 2–8 times whilst cocking tail at c. 45°. Allo-preening of head and neck not recorded, but mutual bill-rubbing has.

COPULATION: (GFA)

NEST: (GFA) Built very quickly (c. 1 day, Brown *et al.* 1982); av (Australia) 3.5 m (0.6–5.7) above water. Made of leafy or other twigs and reeds and varies from flimsy to substantial. Diameter c. 45 cm.

EGG/CLUTCH: Long oval, pale greenish or bluish-white with variable chalky outer layer; sometimes dark brown spots. Calculated weight 35.8 g; measured weight (Africa) 37 g. Measurements (Africa) 53 (46–60) × 35 (31–40) n = 164. Clutch 2–6; mean 3.4 n = 52 (E Africa); 3.7 n = 45 (Ghana); 3.3 n = 622 (Zimbabwe); 3.0 n = 20 (Namibia and

Botswana); 2.9 n = 111 (SW Cape); 2.9 n = 39 (Natal). Australian clutches similar (2–6, mean 4.0). In India usually 3–4, most often 4. Laid at irregular intervals (1–3 days) beginning only a very few days after mating (Johnsgard says ‘2–3 days after pair-bonding’, whatever that means).

REPLACEMENT LAYING: No details.

INCUBATION: (GFA) Australian av 28 days (26–30), successively laid eggs hatching at intervals of up to 3 days. Shifts 2–6 hours.

CHICK/BROOD: Hatchling naked with dark skin. After 2 days *rufa* covered with white down, later turning buff-brown on head, neck and mantle (may be entirely brown). Primaries, secondaries and tail feathers erupt c. 3 weeks and well developed at 4 weeks. *Melanogaster* at first white. *Novaehollandiae* down pale buff underneath, darker brown above with (maybe) white stripe on side of head and upper neck. Eye dark grey or blue-grey; bill pale horn; gular skin yellowish. Legs and feet white to flesh. Brood av 3.0 at fledging (Australia), means 1 egg or chick usually lost from av clutch of 4.

CARE OF YOUNG: See anhinga.

BEHAVIOUR OF YOUNG: See anhinga.

FLEDGING: At 25–40 days darters may leave nest and swim and dive nearby, either returning to nest to be fed, using bill, wings, and feet to climb or merely perching with other young on lower branches. African darters, at least, rarely return to the nest after 5 weeks. ‘Fledging’, whatever that means, occurred at 58 days in 3 captive African darters (Junor 1972).

POST-FLEDGING: Apparently (Australia) may disperse before 2 months and not known to be accompanied or fed after that.

BREEDING SUCCESS: (Ghana, Bowen *et al.* 1962) Hatched from laid: 89% (n = 15 nests), 58% (n = 13). Fledged from hatched: 72% (n = 15 broods); 40% (n = 13). Fledged from laid: 64%, 23%. In Australia av brood at fledging 3.0 but overall success vitiated by disturbance.

FIDELITY TO COLONY, SITE, AND MATE: (GFA)

AGE OF FIRST BREEDING: Old record of ability to breed at 1 year whilst still in immature plumage requires to be confirmed, since anhinga first breeds at 2 or more years.

NON-BREEDING AND MORTALITY: No details.

Frigatebirds

Ascension Frigatebird *Fregata aquila*

PLATE 11

Pelecanus aquilas Linnaeus, 1758, Ascension Island.

Other common names: man-o'-war, sea-hawk.

French: frégate aigle-de-mère. German: adlerfregattvogel. Spanish: rabihorcado de Ascension.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: All black with green and purple sheen; mainly bluish-green on lanceolate head-feathers, bottle-green on those of back. No obvious alar bar. Shafts of wing-quills dark but of tail ivory white. Some, presumably young, breeding individuals have white breast and abdomen or reticulate patterns of white on black, or even white abdominal patches. Iris brown; eye-lids, eye-ring, feet, legs black. Courting males have crimson, inflatable gular pouch forming heart-shaped balloon.

ADULT F: Black with rusty brown especially on neck and breast band, but some individuals have white breast and abdomen or (as male) reticulate pattern. Alar bar present. Feet pink or coral red. Eyelids, eye-ring pale blue.

POST-NUPTIAL: Little change except male loses gular pouch.

JUVENILE AND IMMATURE: White head, neck, abdomen, sometimes flecked with rust, gradually

become mottled black. Prominent alar bar. Feet, eyelids, orbital ring acquire bluish tinge.

Field characters

Adult male may be indistinguishable from magnificent frigatebird. Typical females only female frigatebirds to lack white and to possess brown 'collar' and breast band. Juvenile notably pale on head and lower breast but this not enough to distinguish it from all great frigatebirds. White axillary spur of Ascension juvenile absent in great but occurs in lesser. Alar bar not diagnostic.

Measurements (see Appendix)

Voice

Few details. Males clomp bill violently during gular presentation but apparently lack vocal warble; females descend with high-pitched clucking cry. Begging young squeal and groan.

Range and status (Figure 6.153)

Endemic to Ascension Island (S Atlantic). None now on main island though formerly common. Confined to Boatswain Bird Island where Stonehouse and Stonehouse (1963) estimated 8,000–10,000 breeders, 1,000–2,000 juveniles and immatures. Ashmole *et al.* (1994) give <10,000 for total population.

MOVEMENTS: Outwith breeding, recorded from surrounding waters but rarely elsewhere (vagrant Africa).

Foraging and food

Little specific information. Indications that foraging stints may be comparatively short though some lasted more than 2 days. As in other frigatebirds adults seldom together at nest. Food mainly flying fish *Exocoetus* and probably *Cypselurus* and *Hirundichthys* and squid. Highly predatory on small chicks of other seabirds (e.g. sooty terns) and, when colony disturbed, of own species. Takes young turtles. No information on importance of kleptoparasitism but occurs in adults and immatures.

Habitat and breeding biology

(See Fig. at end of ch. 5; Stonehouse and Stonehouse 1963)

HABITAT: Breeds among boulders, outcrops, and guano of island's basalt cap. Prefers uneven slopes, presumably for take-off.

COLONY: In groups of 12 or more, varying in density though often 'dense' (2–3 nests per m²). In June 5.6 per 50 m² rising to max 25.4 in Oct.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Cannot complete breeding cycle in <15 months min and successful breeding therefore unlikely to be >1 in 2 years. If 'rest' years occur (probable) breeding frequency further reduced. Main courtship April–Aug but seen every month, though few Feb–May. Laying peaks in Oct, but



6.149 Juvenile Ascension frigatebird seizing wideawake chick. (Photo: N.P. Ashmole.)

can occur any month. Thus seems somewhat less seasonal than most frigatebirds.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Gular presentation by males communal and similar to other frigatebirds', except display on ground, using same rhythmical throbbing with extended and vibrating wings between which upward pointing head and inflated crimson sac directed at overflying females. Bill clapped loudly. Males sometimes ignore overflying female which may suggest male selection of potential mate, just as females may ignore displaying male. After female has landed, interaction of pair similar to other frigatebirds. Though not explicitly stated by Stonehouses, obvious that males may move between display groups. Once pair formed, however, continuous site-guarding by one member essential if site to be retained. Yet, because of male movement from unsuccessful display site to another, impracticable to establish and defend definitive one before pair has formed. Therefore before pair-formation no overt fighting or ritualized defence of site. Even after pair-formation site-defence comparatively undifferentiated, spasmodic, and low-key.

COPULATION: (GFA)

NEST: (GFA) Mere scrape, with pebbles, bones, and feathers.

EGG/CLUTCH: Always one; white, thin-shelled and fragile: 6.78 (5.97–7.45) × 4.71 (4.30–4.94) n = 96. Weight 75.8 (47–92 though lower extreme must be well-incubated egg). Fresh weight at least 6% adult weight.

REPLACEMENT LAYING: Claimed but equivocal. Probably rarely relays but apparently a few birds, particularly males, which lose new eggs, may take over neighbour's egg, so confusion about whether re-laying had occurred seems possible (male identifiable but perhaps site not).

INCUBATION: Shared about equally; 43–51 days n = 12 (mainly 43–6) mean probably c. 44. Shifts 24–48 hr—no details of max.



6.150 After successful 'advertising' by the male (gular presentation) the pair spend time together consolidating their bond. (Photo: N.P. Ashmole.)

CHICK: Hatches naked and helpless but not blind; weight c. 55 g. Skin, bill, legs and feet pale blue. Closely brooded for up to 10 days and may be attended for further period though said to be left unguarded as early as 12 days even though extremely vulnerable (see Care of young). Down appears days 6–10; back feathers, scapulars erupt days 21–5 and grow rapidly. Tips of secondaries appear 31–40, primaries days 41–50. Tail feathers appear days 51–60. Down clears from wings days 81–100, from head days 101–20 but not clear from body, especially flanks, until days 140–80. Approx adult weight attained by 16 weeks. Stonehouses gives 9 easily recognizable stages in development; probably roughly applicable to other frigatebird species.

CARE OF YOUNG: Shared. Some indication female does most brooding small young. Seldom leave

young unattended until more than 10 days (surprising if young so small are unattended unless adults disturbed).

BEHAVIOUR OF YOUNG: No details.

FLEDGING: No precise details on first flight. Begins to fly by 6th or 7th month.

POST-FLEDGING: Fed for several months; unlikely to be less than other frigates. Juveniles practise foraging even though still being fed by parents; often go beyond sight of island. May take young seabirds and pirate incoming boobies.

BREEDING SUCCESS: Hatched from laid: 40% (n = 166). Fledged from hatched: <36% (n = 24) (early losses not included). Fledged from laid: 14%

($n = 166$), 6% ($n = 33$), 48% ($n = 31$). Survived to independence: no figure. Success declined as season progressed and lower in main breeding area where most disturbance by non-breeders and by humans. Indicates loss of eggs and chicks due mainly to social factors, principally interference by conspecifics. Not due to food shortage or predation by other species. Losses of eggs and small chicks greatest in areas of densest nesting. Success highest in areas where nests started earlier than peak of laying. Nests started late may have suffered from reduction in food. This species confirms general

tendency of frigatebirds to lose eggs and chicks through conspecific interference.

FIDELITY TO COLONY, SITE, AND MATE: Endemic to Ascension. No retention of site or mate in successive breeding attempts, excluding possible replacement layings.

AGE OF FIRST BREEDING: (GFA)

NON-BREEDING YEARS: Probable; (GFA).

LONGEVITY AND MORTALITY: Unknown: (GFA).

Christmas Frigatebird *Fregata andrewsi*

PLATE 11

Fregata andrewsi Mathews, 1914, Christmas Island, Indian Ocean.

Other common names: Christmas Island, Andrew's, man-o'-war, sea-hawk.

French: frégate d'Andrews. German: werbauch-fregattvogel. Spanish: rabihorcado de la Christmas.

Sub-species

Monotypic.

Description

ADULT M PRE-BREEDING: Very large, black upperparts with green/purple gloss, lanceolate nape,

mantle, scapular feathers. Pale alar bar. Black beneath except for large white patch on lower abdomen. Bill dark, iris brown, eye-ring black. Crimson gular sac. Legs pinkish, feet black above with pale soles.

ADULT F: Back much as male but white from vent to throat, extending as broad collar round sides of neck and into armpits. Head, neck, throat black, giving conspicuous black-hooded-and-bibbed effect. Pale alar bar more conspicuous than in male. Bill, eye-ring, feet pink.

POST-NUPTIAL: Little change; male loses gular sac.

JUVENILE AND IMMATURE: Resembles female but with fawn head (some russet here and on neck). Broad black pectoral band; lower breast white, in some birds extending onto black underwing. Bill pale, eye-ring, legs, feet dark. Later russet fades; bill, feet, legs become bluish or pink. Head, throat whiten year 2 whilst black pectoral band disintegrates. Adult plumage may be attained year 4.

Field characters

Adult M readily distinguished by white patch on abdomen; F by large size, conspicuous white collar, white axillary spur and extensive white underparts. Juv identification impracticable but late immatures easier. Yellowish rather than reddish on



6.151 Distinctive pattern of white on the underparts of the female Christmas frigatebird.



6.152 Male Christmas frigatebird with deflated sac.

head and neck; large size, pale bill distinguish it from great, most likely species to overlap. Immature males have white abdomen (cf. some black in great and lesser). Immature females have white on abdomen whereas lesser has black and is smaller, though has white axillary spur. Great no white spur, lacks black throat.

Measurements (see Appendix)

Voice

Mainly silent at sea? Pre-landing call of male disyllabic, rusty 'a-ee, a-ee' followed on landing by trisyllabic descending call. Courtship warble during gular presentation low-pitched and slow 'oo-aw, oo-aw' given to overflying females, during mutual head waving and at end of landing call during courtship. Mechanical bill-rattling, distinct clapping of mandibles with resonance imparted, presumably by pouch, given by males to overflying

females during gular presentation and by courting males as response to intrusion by other males. Distinguished from bill-snapping, prelude to biting and, at all ages, in a variety of alarm situations. Soft vibration of bill during mutual head waving but not, apparently, after egg laid. Adult females give rasping or discordant chatter during courtship. Young beg with porcine squealing. Sonogram in Marchant and Higgins (1990).

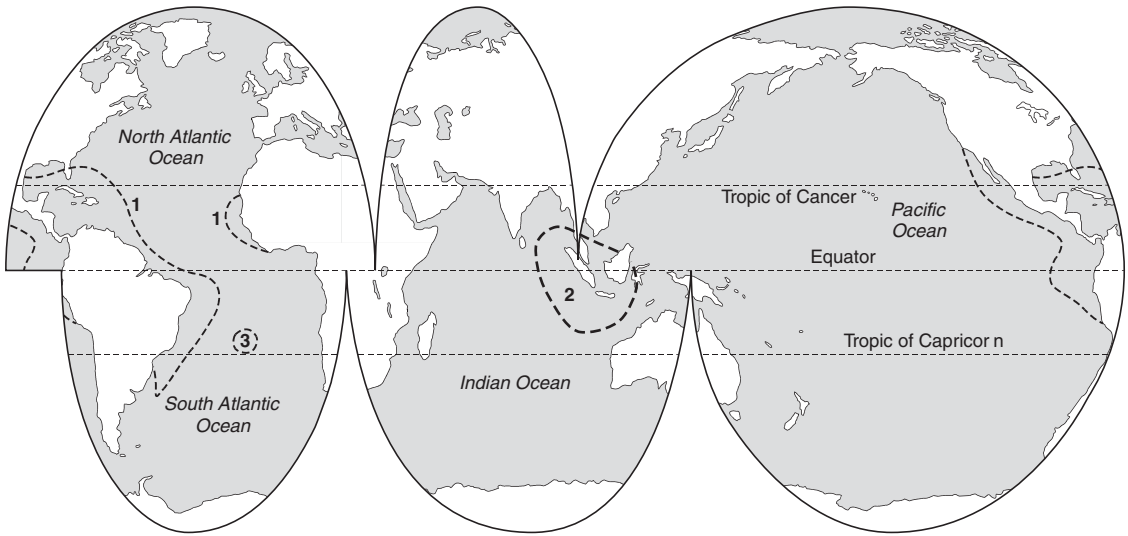
Range and status (Figure 6.153)

Breeds only on Christmas Island (IO); present all year. At c. 1,600 pairs, rarest of 5 frigatebirds. Much persecuted for almost 100 years by resident Malay and Chinese, who killed large numbers of adults (e.g. Nelson 1986). Population must have been substantially reduced and breeding distribution on island altered; e.g. decreased near Flying Fish Cove, original area of settlement at end of last century. Now fully protected (ANPWS) but considered endangered.

MOVEMENTS: Occurs more widely at sea, where immatures doubtless overlooked in Indo-Malay region (Andamans, Nicobars, Sumatra, Java) and occasionally N to South China Sea. Vagrant to Australia and E Africa. Report (Chasen 1933) that common in Andamans led to surmise that might breed there, but no evidence; recently seen there (Saxena 1994). Occasionally at Cocos Keeling, where large colony great frigates.

Foraging and food

As other frigatebirds, but said to have more restricted preference for particular band of sea-surface temperature ($>26.4^{\circ}\text{C}$) and salinity (<34.5) than great and lesser frigatebirds in Indian Ocean. Aerial surface-snatching, scavenging, opportunistic predation and kleptoparasitism, particularly on boobies, now including Abbott's probably more than formerly as consequence of forest clearing which creates open spaces, thermals and 'idling space' above forest where previously few frigatebirds. Food mostly squid or fish (few details) but items such as locusts picked up from land. Habitually drinks in flight from rainwater pools in cleared areas.



6.153 Distribution of 1 magnificent frigatebird 2 Christmas frigatebird (endemic) 3 Ascension frigatebird (endemic). From: B and S Stonehouse (1963).

Habitat and breeding biology

(See Fig. at end of ch. 5; Nelson 1976; Stokes 1988)

HABITAT: Confined to shore terrace of Christmas Island at 3 specific locations in N and E and discrete from great frigatebirds. Perhaps 65% or more of nests located in *c.* 40 ha behind golf course (Stokes 1988) which June–July 1985 (peak numbers) held *c.* 854 occupied nests. Often nests in partly dead trees with little shade, chiefly in *Terminalia catappa*, *Celtis* spp. and *Ficus*, 7–30 m above ground or less if tree on precipitous site.

COLONIES: In groups of 10–20 nests (several in one tree) adjacent nests sometimes 1 m or less apart but usually irregularly spaced.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Breeds once in 2 years or even less frequently if non-breeding years taken. Courtship may begin late Dec and continue till April, mainly Feb–March. Eggs laid mid-Feb to June, mainly March–April, 90% early March–mid-May.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Essentially as others but males tend to cluster less closely and may display singly in breaks

in canopy. Display-site defended by bill-grappling, snapping and even fighting though this must be hazardous and uncommon. Components of courtship, principally gular presentation, may be used in defence of site. Display groups extremely noisy, deep ‘ee-ow, ee-ow’ of male carrying far. Just as warble given during gular presentation slower and deeper than in great frigatebird, so wing-trembling less rapid, though wings widely spread, with silvery undersurfaces turned upwards. Bill-rattling common during gular presentation. Display mainly begins in late Jan with pairings mid or late Feb and most eggs early March. No precise information on movements of males between display groups nor on duration of unbroken attendance shifts at display stations.

COPULATION: (GFA)

NEST: (GFA) Variable; often extremely loosely woven. Excreta cements. May disintegrate before chick fledges.

EGG/CLUTCH: Always one, elliptical, smooth, thin-shelled, white. Weighs 82 g (78–88) or 5.3% female’s weight.

REPLACEMENT LAYING: Said to occur but no details.

INCUBATION: Shared, *c.* 54 days. Shifts, male 5.5 (1–11) days; female 6.6 (2–14) (Reville in Marchant and Higgins 1990)

CHICK: Nidicolous with pinkish skin and bluish bill, legs, and feet. White pre-plumule down which covers body by end week 2 and is replaced by coarser down, pale smoky grey on dorsal surface and back and sides of neck. Feathers on dorsal and scapular areas erupt in week 4 or earlier. Tips of secondaries appear week 6 and primaries and tail feathers a week later. At 2 months nestlings densely covered with down and scapulars form neat black cape. Feathers replace down between 80 and 100 days on wings, *c.* 3 weeks later on head though traces remain till *c.* 140 days and *c.* 180 days on belly and flanks. First fly *c.* 6 months. Adult weight *c.* 25 weeks (GFA). Brooded and guarded by both parents alternately for *c.* 42 days (30–57).

CARE OF YOUNG: Shared. (GFA)

BEHAVIOUR OF YOUNG: No specific details.

FLEDGING: Details of first flight not recorded. Fledging period *c.* 177 days (134–258) (Stokes 1988) but both extremes unreliable.

POST-FLEDGING: Fed for *c.* 197 days (140–255). If these extreme figures valid, a breeding cycle could occupy 360–600 days; more likely figure *c.* 450 days. In any event, since both sexes feed free-flying young neither male nor female could breed more often than once in 2 years.

BREEDING SUCCESS: (Stokes 1988) Hatched from laid: 80% (*n* = 84). Fledged from hatched: 68%. Fledged from laid 55%. Survived to independence: 42% of fledged young, or 35% of hatchlings or 28%

of eggs laid. Compares favourably with most other figures for frigatebirds. Losses before flying due to: high winds (9 nests with eggs blown down), desertion (in 2 cases a partner failed to relieve its mate and in another nest taken over by usurping male), 12 chicks lost in first few weeks after hatching (1 at hatching, 3 starved when one parent failed to return, 1 displaced by usurping male and 1 nest abandoned for unknown reason). After fledging, 3 disappeared in cyclone, 2 found starving beneath nesting tree and 17 disappeared within first 3 months during which many already starving. In most years starvation of free-flying but dependent young during Jan–March likely to be main cause of death. Accords with situation in Abbott's booby and probably associated with seasonal rise in sea-surface temperature and concomitant scarcity of food for adults and hence for dependent young. Juveniles probably do not forage far afield at this time.

FIDELITY TO COLONY, SITE, AND MATE: Remain broadly within certain restricted areas of Christmas Island on shore terrace, but groups of nests not consistently located in these areas. Almost certainly bonds between partners not retained in successive breedings, and sites change also.

AGE OF FIRST BREEDING: Not known but guessed to be at least 5 years and probably considerably more.

NON-BREEDING YEARS: No information but likely to occur.

LONGEVITY AND MORTALITY: Low productivity means high life-expectancy, perhaps 25–30 years or more. Annual adult mortality rate not known but conjecturally, and excluding killing by man, 3% or less.

Magnificent Frigatebird *Fregata magnificens*

PLATE 11

Fregata minor magnificens Mathews, 1914, Barrington Island, Galapagos.

Other common names: Caribbean man-o'-war, hurricane bird, scissors tail.

French: frégate superbe. German: prachtfregattvogel. Spanish: rabihorcado magnifico, tyera, rabijunco, anunciador.

Sub-species

F. m. magnificens Galapagos. *F. m. lowei* Cape Verde and African coast. *F. m. rothschildi* Antilles, Atlantic and Pacific coasts America. Races supposedly separable by measurements, endorsed by Murphy (1936) but del Hoyo *et al.* (1992) say not generally accepted. No described colour differences between populations.

Description

ADULT M PRE-BREEDING: All black with metallic purple gloss on lanceolate feathers of back and scapulars, green on head and wings. Alar bar can be inconspicuous or broad and pale. Crimson gular sac. Bill darkish grey or lead blue often with paler tip. Iris dark brown, eye-ring, legs, feet black.

ADULT F: Upperparts, head blackish, but browner than male, with some gloss. Conspicuous alar bar. Black-brown throat extends down front of neck in V-shape. Pale nuchal collar somewhat pale and indistinct. Breast, sides of abdomen white. Abdomen, under-tail coverts blackish. Bill grey-blue or pinkish, gular skin dark, eye-ring blue, iris dark brown. Legs, feet reddish,

POST-NUPTIAL: Little change; male loses gular sac.

JUVENILE AND IMMATURE: (Howell 1994) Head, neck, most of underparts white with variable amount pale ginger on sides of breast. Upperparts blackish with rusty tinge. Breast-band irregular and blackish, as also flanks and vent. Pointed black chest side wedges, rarely meeting in centre, enclose white diamond-shaped belly patch. Alar bar broad and pale. Bill light grey-blue, pinkish at tip. Eye-ring pale grey-blue, iris brown. Legs, feet dull pinkish. Juvenile-type head and body plumage probably kept until 18–24 months (Howell 1994). Adult plumage acquired by series of moults; variable retention of feathers makes stages imprecise (see Figure 5.35).

Field characters

Although larger (both sexes overall wingspan 210–40 cm magnificent, against 198–220 cm great), adult male can be impossible to distinguish from Ascension or great frigatebirds at sea, where feet hidden. Often appears relatively longer-tailed than great; magnificent tail = 43–51% total length against 41–7% in great but no use for identifying lone bird. Also may appear slightly less stocky than great. Lack of alar bar perhaps *not* completely trustworthy, although Howell examined more than 1,000 adult male magnificents and all lacked any trace of alar bar. Axillary feathers tend to have light tips giving scalloped

appearance to ‘armpits’ but not diagnostic (Howell 1994). Adult female has black chin and throat which female great lacks. Magnificent female more resembles female lesser, though magnificent’s white nuchal collar narrower and less distinct and difference in size may be evident. Juvenile notably white about head with less conspicuous breast-band than great, but later immature stages probably not safely distinguishable (Figure 5.35).

Measurements (see Appendix)

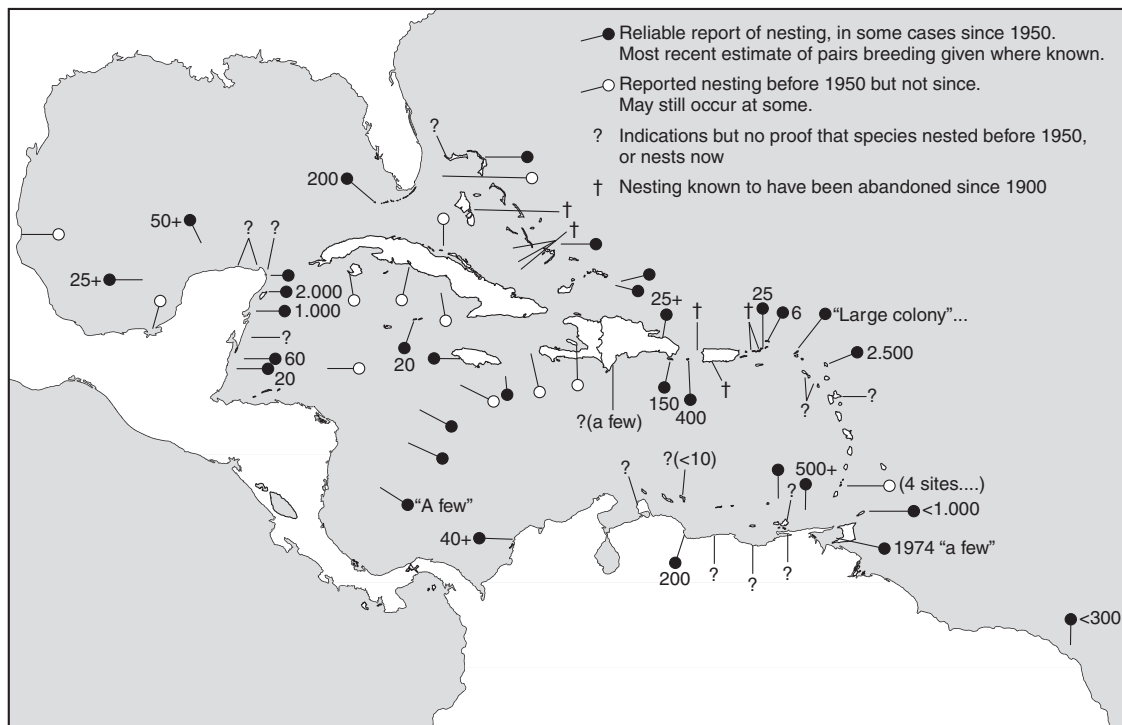
Voice

Landing call, both sexes, rapid rattle descending in pitch and increasing in speed, deeper and hoarser in female. Displaying males ‘drum’ and ‘reel’, latter being equivalent to same call in great frigatebird. Lacks warble of great and Christmas. Young beg with typical harsh squealing.

Range and status

(Figure 6.154; summary del Hoyo *et al.* 1992)

Tropical and sub-tropical seas and coasts but with most restricted distribution of 3 commoner frigatebirds. Del Hoyo *et al.*’s suggestion of ‘probably several hundred thousand birds’ may be highly optimistic. Primarily new-world species mainly on Atlantic coasts of Americas and in Caribbean (*c.* 25 colonies, maybe 8,000 pairs), and South America to Brazil (*c.* 2,000 nests Cagarra Is, 700 pairs Currais Is) and E to Cape Verdes. Ranges to adjacent African coast. Old records of nesting in Florida uncertain but confirmed in 1969 (*c.* 100 pairs on Marquesas Keys) where, in 1975, still *c.* 100 active nests. Pacific outpost in Galapagos and stations in Baja California, Mexico (3 colonies, *c.* 60,000 pairs, W Mexico) Panama, and Ecuador. Murphy (1936) related breeding range to presence of suitable mangrove habitat. Overlaps with great frigatebird in Galapagos but does not form mixed colonies; prefers central islands whilst great frigatebird prefers outer ones. Because of comparatively restricted distribution, often in areas subject to human pressure, probably less secure than great and lesser frigatebirds, though not currently threatened. However, disturbance, leading to



6.154 Breeding distribution of the magnificent frigatebird in the Caribbean (8000+ pairs). (From Halewyn and Norton 1984.)

panic and entanglement of adults, and loss of eggs and chicks, together with slaughter by fishermen at colonies and roosts particularly in Caribbean (for their oil, reputedly medicinal or for bait) and introduction of cats and rats, causes for concern.

Frigatebirds depend on wind for flight and female magnificents, being heavier than males, may be over-represented in areas of higher wind-speed, thus leading to differences in sex-ratio in different areas. 'Thermal streets' above ocean might affect distribution (Harrington *et al.* 1972).

MOVEMENTS: Resident in breeding areas, but pre-breeders and (presumably temporary) non-breeding adults disperse considerable distances. Regularly visits tropical waters (Atlantic and Pacific) of American coasts where does not breed. Suggestion (Palmer 1962) that disappearance of birds on coasts of Gulf of Mexico correlates with timing of breeding at sites in Caribbean and Bahamas.

Foraging and food

May rise to considerable height at dawn and sail out to sea in long, spaced line, returning similarly in evening. Will feed in mixed-species flocks including (Galapagos) boobies, shearwaters, terns, and the flightless Galapagos cormorant and penguin (Mills 1998). May benefit from pursuit divers driving fish to surface. Tends to scavenge at man-made food sources such as docks and sewers more than others. Opportunistically predatory, taking eggs and young seabirds (e.g. sooty terns, red-footed boobies) and turtle hatchlings. Kleptoparasitic on pelicans, cormorants, gulls, terns, osprey, and even conspecifics which have caught their fish honestly (Palmer 1962) (GFA). Food includes jellyfish and plankton besides usual flying fish (Exocoetidae) and squid (Ommastrephidae, 5–11 cm). In Baja California main food *Sardinops* sp (Carmona *et al.* 1995). Will take freshwater fish.

Habitat and breeding biology

(See Fig. at end of ch. 5; most detailed Diamond 1973; Palmer 1962; Coello *et al.* 1977; Trivelpiece and Ferraris 1987; Carmona *et al.* 1995)

HABITAT: Offshore and coastal islands or islets usually in lagoon-fringing or other vegetation, commonly mangroves *Avicennia* though will nest in tall trees, flat-topped shrubs, tussocks, rocks, or even bare ground. As with great and lesser frigatebirds, even if colony itself exposed to wind, nests often on sheltered side of tree so that approach and landing initially upwind. Landing has to be precise but take-off comparatively easy. Breeds and feeds with other seabirds such as pelicans, boobies, and cormorants. Seems to avoid muddy waters such as those off NE Brazil but nevertheless does penetrate estuaries. May even occur over freshwater lakes. Rarely reported far from land but may be due identification problems.

COLONIES: Handful–c. 2,500 but as in other frigatebirds nests occur in clusters, many in one tree and none in others. Nests may be close enough for owners to bill-fence. An exceptional record (in Palmer 1962) of nests on bare rock at estimated density of 1.3 nests per m² which must be absolute max. On Barbuda Diamond (1973) found them in isolated clumps at min density of 0.28 nests per m², 0.3–2.6 m above ground. On Belize min estimate nest density 0.87 per m² (0.53–1.36); Bahamas 1.35 per m².

FREQUENCY, TIMING, AND DURATION OF BREEDING: Apparently uniquely among frigatebirds, males abandon chicks aged 3–4 months, disperse and moult, and then possibly begin new cycle with another female leaving first one to complete feeding of young, including long post-fledging period (Diamond 1973). This was confirmed in Galapagos (Coello *et al.* 1977), Belize (Trivelpiece and Ferraris 1987) and in Baja California (Osorno 1999) where all males deserted when chicks 19–160 days (questionably enormous range), mean 77 ± 5 . Chicks deserted when very young had higher probability of dying. Late deserting males

less likely to be seen with gular sac following year. Thus females can manage at most only one successful cycle in 2 years but theoretically males can breed every year. For this to occur, has to be more females than males; sex ratio in Barbuda 1 male per 2 females; Galapagos 2 per 3. Diamond suggests phenomenon depends on rich and predictable food but seabirds on at least some Galapagos islands suffer unpredictably scarce food.

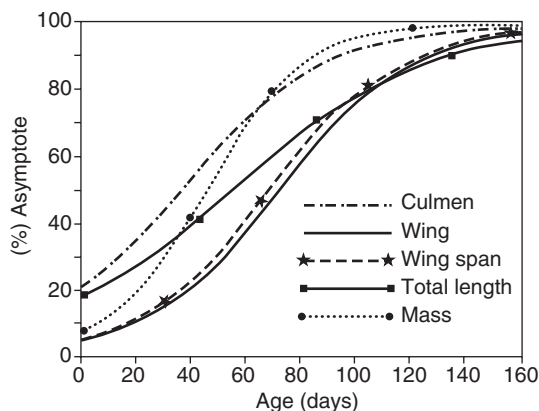
As other frigatebirds, pairs display, court, lay, and incubate alongside others which still have large young. On Barbuda display began late Aug. Egg-laying seasonal but extended: Barbuda Sept–March with peak early Nov, major one early Dec; Baja California 4 laying peaks (weeks 7, 12, 17, 23 Carmona *et al.* 1995); Galapagos laid Feb–Nov with Aug–Sept peak; Belize main laying mid-Dec–early April.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: During gular presentation males alternate 'reeling' with 'drumming' but lack vocal warble. Display groups, commonly 4–8 males performing gular presentation to overflying females who hover and inspect group but without assuming distinctive posture equivalent to 'goose-neck' of female lesser. After female lands, pair head-shake and 'snake' necks over each other, female uttering 'twittering' call. Males perform low-intensity and less stereotyped version of gular presentation towards other males attempting to land nearby but this phenomenon, that is, an aggressive component in sexual display, is commonplace in bird display and does not constitute a separate territorial display. Nevertheless, males clearly tend to settle near to displaying males, presumably because this enhances chance of acquiring female.

COPULATION: (GFA)

NEST: (GFA) Small, frail platform (25 + 6 cm diameter) of poorly interlaced twigs eventually clogged with excreta from young.

EGG/CLUTCH: As others; always one. 68.4 (64.5–74) × 46.5 (43.5–50) n = 50 various localities. 71.3 × 47.8 Belize. 68.94 × 46.37 n = 20 Caribbean.



6.155 Growth of the magnificent frigatebird. (From Carmona, Guzman and Elorduy 1995.)

REPLACEMENT LAYING: Unproven but suspected.

INCUBATION: Shared *c.* 50 days; some change-overs at night. Shifts, few hours to 3–4 days (Galapagos), significantly shorter than great frigatebird in same area, correlated with inshore feeding of magnificent.

CHICK: Much as others. Precise colouring of hatchling undescribed. Growth rate, Figure 6.155. Baja Californian chicks reached asymptotes at: culmen 111.49; wing 1007.2; overall length 942.1; weight 1341 g. Bimodal bill-lengths of Galapagos juveniles allows sexing; M 87–115 mm, F 116–135 mm with little overlap (Coello *et al.* 1977). Bill measurements indicate sex-ratio at juvenile stage of 3 females to 2 males. On Barbuda Diamond (1973) divided fledglings by colour of wing bar (brown in males, white in females) and found former had bills measuring 105.8 (102–11) *n* = 9, and latter 120 (117–24) *n* = 10.

CARE OF YOUNG: Shared but unequally (see below). Closely brooded by either parent equally for first 3 weeks and intermittently attended thereafter during day until 30–50 days old. At 6 weeks, chicks in Baja California unguarded for 50% of daylight hours. Even at 60 days still brooded at night. Both sexes

bring food to young during day or night, males favouring night feeds. In Galapagos 0.72 feeds per day (Oct, chicks 10–20 days old), 0.69 per day (Nov, chicks 1–2 months), 0.422 (Jan, chicks 3–4 months) (Coello *et al.* 1977).

BEHAVIOUR OF YOUNG: (GFA)

FLEDGING: (GFA) 9 chicks on Barbuda av 166 days (149–207); Baja California *c.* 181.

POST-FLEDGING: Fed for *c.* 26–30 weeks on Barbuda, solely by females. Observed 21 weeks after fledging at which time rate had not decreased compared with earlier. In Baja California post-fledging feeding by female lasted *c.* 26 weeks. In Galapagos both parents fed young for first *c.* 16 weeks but for further 16–32 weeks solely by female. In Belize, chicks 10–14 weeks occasionally fed by male but not after week 16. Even chicks younger than 8 weeks fed slightly more by females than by males.

BREEDING SUCCESS: (Barbuda, Diamond 1973; Baja California, Carmona *et al.* 1995) Hatched from laid: 64.3% (*n* = 14, California). Fledged from hatched: 54% (*n* = 90, California). Fledged from laid: 58% (*n* = 58%, Barbuda). Survived to independence: no figures. In California new nests appeared, sometimes on top of abandoned ones, mainly in March and in these nests only 30% of chicks died. Main cause of loss of eggs or small chicks, pilfering of nest material by males (where were parents—disturbed by observers?). Some older chicks killed when wind broke nest branch.

FIDELITY TO COLONY, SITE, AND MATE: No specific information.

AGE OF FIRST BREEDING AND NON-BREEDING YEARS: No details; may first breed at 5–11 years.

LONGEVITY AND MORTALITY: Potentially very long-lived (20–30+).

Great Frigatebird *Fregata minor*

PLATE 11

Pelecanus minor Gmelin, 1789, no locality. Fixed as eastern Indian Ocean by Rothschild 1915 and restricted to Christmas Island by Lowe 1924.

Other common names: greater frigatebird, man-o'-war, sea-hawk. Unfortunate contradiction between latin *minor* and English great.

French: frégate du Pacifique. German: bindenfregattvogel. Spanish: rabihorcado grande.

Sub-species

F. m. aldobrensis Mathews 1914 W Indian Ocean. *F. m. minor* Gmelin 1789 E Indian and SW Pacific. *F. m. palmerstoni* Gmelin 1789 W and C Pacific. *F. m. ridgewayi* Mathews 1914 E Pacific. *F. m. nicolli* Mathews S Atlantic. Several of these sub-species were created by Mathews, a notorious splitter and may be invalid. Geographic variations largely in size (considerable) and, in female, colour of bill and eye-ring. Whilst no female dimorphism found within single population, in Galapagos females have blue bills and pink orbital rings; on Johnston Atoll some females have pink bills and orbital rings; on Aldabra bills and orbital rings always pink and on Christmas Island (IO) bills blue-grey with pinkish base and orbital rings pink. Adaptive significance, if any, of this variation, unknown but no support for idea that it subserves reproductive isolation between this species and lesser frigatebird where, as often, these two breed on same island.

Description (GFA)

ADULT M PRE-BREEDING: Very large, entirely black with metallic green or purple gloss especially on lanceolate nape, mantle, scapular feathers. Brownish alar bar variably conspicuous. Bill dark, grey-blue to blackish with lighter streaks; iris brown; eye-ring blackish. Crimson gular sac. Legs, feet dull pink.

ADULT F: Head, hind neck black forming dark cap which contrasts with grey of chin and throat, black running below eye and along side of neck.

Upperparts black except for buffish alar bar, often very conspicuous. Upper breast, flanks, belly white. Abdomen, vent and tail black. Gular strip light coloured; bill blue-grey or pink depending on region; eye-ring pink, blue or lilac; iris brown. Legs, feet pinkish.

POST-NUPTIAL: Little change; male sac shrivels; alar bar may become less conspicuous, but this not precisely seasonal.

JUVENILE AND IMMATURE: Head, throat, upper neck rusty brown becoming variably paler or mottled; white in some. Changes may begin before independence. Upperparts black with pale, conspicuous alar bar. Black breast band thinnest at mid-point; below this, white. Vent black. Eye-ring dark; iris brown; bill pale grey with mauvish tinge, pale flanges and (often) dark tip to upper mandible. Legs, feet nondescript, darkish. With time, breast band disappears; in immature male head, throat, abdomen blacken, though at first mottled. Upper breast, flanks at first mottled before turning black. In female breast band disintegrates, cap and abdomen blacken and for a time there may be a black band across lower breast. Adult plumage may take at least 5 years to acquire by series of moults; variable retention of feathers makes stages imprecise (see Figure 5.35).

Field characters

Adult male could be extremely difficult to distinguish from Ascension or magnificent frigatebirds, since blackish feet of two latter could be hidden. Best character would be alar bar of great, lacking or less conspicuous in other two. Magnificent often appears longer-tailed than great (Howell 1994) but some overlap. Region in which seen could be best guide. Males of other two species have diagnostic features. Adult female distinguishable by whitish-grey or dusky-grey chin and throat giving capped appearance also black 'armpits'. Females of all others have distinguishing

marks, mainly different distribution of white on neck, underparts and in axillary region. Immatures could be inseparable.

Supposed greater stockiness of great compared with magnificent may be useful to experienced observer.

Measurements (see Appendix)

Different populations differ in size, proportion and weight.

Moult (GFA)

Many breeders in interrupted moult (personal observation) and some start moulting again towards end of breeding cycle (Coello *et al.* 1977).

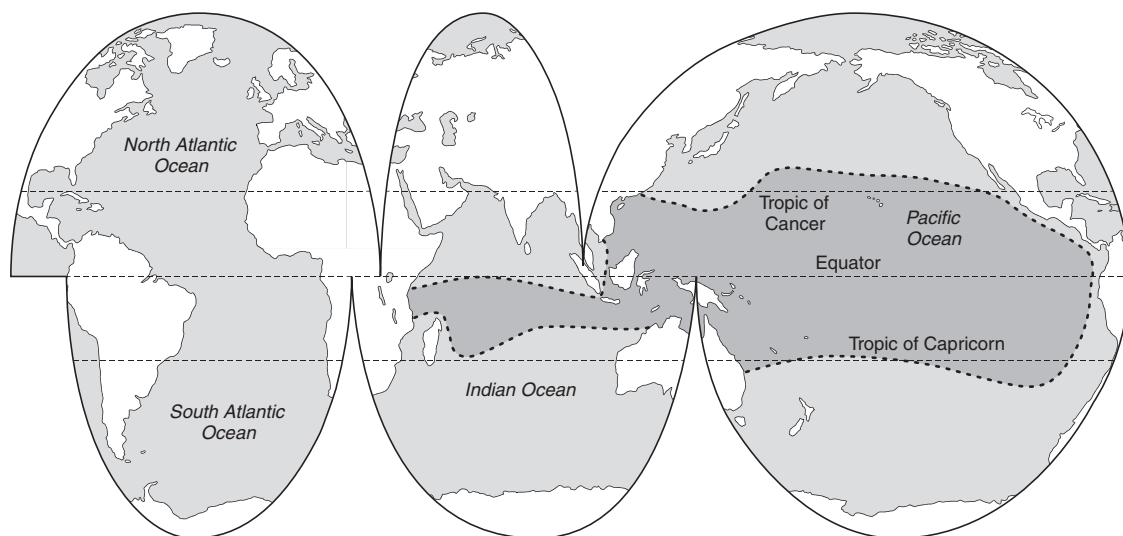
Voice (GFA)

Mainly silent at sea but may utter grating calls when excited at communal food source. At breeding colony males performing gular presentation utter falsetto warble 'hoo-oo-ooo-oo' maybe running into bill-rattling and reeling. Male may warble after female has landed, during head-waving. Female does not warble. Bill rattling more aggressive than sexual, as during M-M interactions. M landing call at site or site plus F an accelerating 'teu-teu-teu' or 'keek-keek-keek'. F lands with

hoarse repetitive 'chuck'. Both sexes snap and rattle bill.

Range and status (Figure 6.156)

Impossible to estimate world numbers since breeds on numerous small and remote islands (del Hoyo *et al.* 1992 suggest 500,000–1,000,000 birds). Overlaps greatly with lesser. Essentially Indo-Pacific with small Atlantic population off Brazil at Trinidad and Martin Vas. In Pacific breeds further N than lesser, spanning 50° Lat between Hawaii and Pitcairns. Substantial population Christmas Island (PO) but Phoenix Island still has best colonies in world and large colony French Frigate Shoals. In E Pacific breeds in Galapagos (where no lessers but some magnificents) 2,000–3,000 nests on Tower Island. Present year-round on Malpelo, with magnificent, and may breed (Pitman *et al.* 1995). Breeds Cocos Island and on Isla San Benedicto in Revillagigedos (where also magnificents). In W Pacific occurs on numerous islands. On Marianas, first documented 1995 (see Lusk *et al.* 2000), population small (A. Kepler personal communication). In Coral Sea breeds on several islands of Great Barrier Reef, along with lessers. In far N of this region 'less common (than several other seabirds) and local' (Blaber *et al.* 1998). In



6.156 World distribution of the great frigatebird.

Indian Ocean breeds only from Maldives (5°N) to Adele Island (15°33' S), a more restricted range than lesser. More numerous on Europa (Madagascar) than formerly thought (700–1,100 pairs, Le Corre and Jouventin 1997b). Breeds, also, Comores (Lovette 1988). Indian Ocean colonies may contain thousands of pairs as on Aldabra (population of great and lesser *c.* 13,000 pairs; distribution Diamond 1971) and Cocos Keeling. Breeds on Christmas Island (IO) (*c.* 3,250 pairs) where it overlaps with Christmas frigate; few if any breeding lessers. Difference in size of birds from different colonies suggests little mixing though this may not apply to colonies within a common foraging range.

Extent of decline within recent times due to massive loss of eggs and small chicks through human disturbance and locally significant mortality of adults killed by fishermen and others may still be masked.

MOVEMENTS: Widely dispersive, juveniles occasionally moving up to several thousand km from breeding area; adults more local, though still wander widely.

Foraging and food (GFA)

Breeders probably usually forage within *c.* 100–200 km of colony during 1–2 weeks or more off-duty intervals. Commonly participates in mixed feeding flocks (boobies, terns). Kleptoparasitic and variably predatory around breeding colony (GFA). Adult females responsible for 64% predation on brown noddy chicks (French Frigate shoals) but no adult males seen hunting (Megyesi and Griffin 1996). Frigatebirds estimated to account for 95% of mortality of brown noddy chicks less than 24 days old. Hawaiian islands, 284 regurgitations av 104 ml by volume and 4.5 prey items—85% fish, 14% squid, 1% juvenile sooty tern (Harrison *et al.* 1983). 23 fish families identified. Prey length av 83 mm (12–272). Reliance on flying fish and squid shown here is typical elsewhere in range (details fish sp and size in Marchant and Higgins 1990). Known predator of sea turtle hatchlings, but on French Frigate Shoals (where 90% of all Hawaiian green turtles breed and large frigate colony) no evidence of hatchlings in 200 stomach contents (Niethammer *et al.* 1992).

Habitat and breeding biology

(See Fig. at end of ch. 5; Galapagos, Nelson 1976; Aldabra, Diamond 1971, 1975a; Reville 1980, 1988)

HABITAT: Isolated oceanic islands, atolls or rocks at sea-level or quite high (>150 m on Christmas Island, IO). On tiny islets e.g. central Pacific, may be few up to >1,000 pairs. Versatile; nests in tall trees, mangroves, low scrub, on rocks, ledges or even on ground, but favours mangroves, usually in intermediate canopy. On Aldabra, utilized only mangroves (3 species) but avoided *Avicennia*. Often in low, flat-topped *Cerriops*. On Tower used xerophytic scrub often 1 m or less high. Lightness and huge wings allow easy take-off except in calm, so extensive free-fall rarely needed.

COLONIES: May change location of sub-colonies within general breeding area from year to year but appears to remain faithful to particular islands. Nesting groups usually 'pure' but in context of wider colony may mix with lessers. Often associates with red-footed booby. Dispersed in clumps, typically 15–20 though widely variable; solitary nests do occur. On Aldabra sub-colonies contained 200–2,000 nests. Within each clump physical factors usually impose irregularity although distance of 0.6–1.4 m between nests seems typical (for further comparative details see under lesser). Clumps stem from preceding male display clusters (Chapter 2) and each tends to be synchronized.

Nesting birds subject to considerable and puzzling interference from unpaired (apparently adult) males with consequent loss of eggs and small young. Coello *et al.* (1977) note immatures rarely seen at colony (Galapagos) which suggests away for several years.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Complete breeding cycle takes >400 days, often much more, and in no population of this frigatebird has a successful female been known to lay in consecutive years. On the contrary, successful pairs probably rarely lay even as often as once in 2 years since they may rest 3 or 4 years after breeding successfully (de Vries 1984). Post-breeders and unsuccessful ones may leave colony, though degree of dispersal varies with locality. Definitely seasonal

though laying protracted and may, over entire range, occur in any month, most rarely Nov–Dec. On Christmas Island (IO) display begins late Dec or early Jan and egg-laying peaks March–April. Christmas Island (PO) laying peaks April–May (spread Jan–Aug). On Aldabra peaks Aug–Oct (spread June–Dec). On Tower (Galapagos) main laying Feb–May. Significantly, this species unaffected by 1986–87 ENSO which had hugely deleterious effect on some species (Anderson 1989b). High degree of seasonality in some colonies, some years, shown by 97% of 317 nests holding eggs in early May, Christmas Island (PO) 1967.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: (GFA) During laying season large colonies marked by hundreds or even thousands of males,

continually aloft. Displaying males on putative breeding-sites present distended gular sac to overflying females, who select a particular male, ignoring some or landing and quickly leaving. Evidence (none so far) that she tends to select previous partner would be of great interest. Pattern of white on ventral surface distinguishes overflying adult female, even when high, from immatures and other species. Males ‘track’ females by swivelling and orienting display to her. Bill-rattling said to be directed only at overflying birds whereas warbling and reeling continue after she has landed near to him. Pair-bond may fail after a few hours or even after several days, sometimes due to interference from an intruding male. As in other frigatebirds, poverty of pair-interactions after pair-formation presumably has to do with impermanence of bond.



6.157 Male advertising display (gular presentation) in the great frigatebird.

COPULATION: (GFA)

NEST: (GFA) May be exceedingly frail or substantial platform of twigs, dead or leafy, but always loosely woven and flat. Guano eventually cements nest material. Measures 29–33 × 26–9 cm across, Aldabra $n = 4$.

EGG/CLUTCH: Always one; 67 × 47.4 Aldabra $n = 8$; 68 (64–71) × 48 (46–59) $n = 7$. Weight: 81 (66–90) Aldabra $n = 9$; 85 (69–96) Galapagos $n = 29$; 5.2 and 5.7% female's weight.

REPLACEMENT LAYING: Quantified (Galapagos) as 12 (4–21) days $n = 13$ and 16 (2–24) $n = 12$ less accurately determined, but absence of individually recognizable birds means case unproven and lower figures very probably incorrect. Indeed, in view of Reville's (1980) study of marked birds in which all apparent replacement laying due to new pairs, safer to conclude that re-laying does not normally occur.

INCUBATION: Approx 55 days, shared; change-over may occur at night. Shifts variable but always long enough to allow protracted foraging; Aldabra 6.4 days (4–13); Christmas Island (PO) $c. 4$; Galapagos 7–17. May lose $c. 20\%$ weight during a shift.

CHICK: Nidicolous. In Galapagos skin pale pink; bill, legs, and feet livid bluish; egg-tooth persists for $c. 1$ week. During week 2 chick becomes covered with scrubby white down, thicker on rump, though gular area remains bare; down becomes long on crown and short, brown on forehead through to ear-coverts and thicker on body. At $c. 3$ weeks dorsal and black scapular feathers first emerge, erupting 5 or 6 days later to provide 'cape'. Day 42 upper wing-coverts; days 56–60 secondaries and tail feathers and days 60–70 primaries erupt. Growth distinctly slower than that of larger Christmas frigate. Growth curves Figure 5.43. Asymptote for bill growth 120 days (cf. 140 for lesser, both on Aldabra). Coello *et al.* (1977) indicate that bimodal distribution of bill lengths in fully grown young can be used to sex individuals with little overlap (males up to $c. 101$ mm, females more than 105 mm). By time chicks large, sex ratio

about equal in Galapagos but on Aldabra Reville suggests more males than females. This might accord with species' tendency for males to display in clusters and females to be highly selective (female choice) but matter remains open.

CARE OF YOUNG: Chick-rearing shared. Closely brooded by either parent for $c. 2$ weeks and guarded until about 4–5 weeks old (22–48 days, mean 34, Aldabra 1976) in shifts of 1–2 days. Immediately after hatching fed frequently (3 or 4 times per day) reducing to 1 in two days or considerably less frequently when older. Chicks 2–4 months 0.44 feeds per day (Galapagos, October), 4–6 months 0.36 per day (December) (Coello *et al.* 1977). Fed mainly in afternoon and more often by female than by male, but may be fed at night, particularly by male, who then broods during morning. Beebe (1928) remarked that as his boat approached Tower Island, Galapagos, hundreds of female frigatebirds kept company overhead with not a single male among them. Calculated intervals between feeds on Aldabra $c. 2.4$ days and ratio of male: female feeds 32:53.

BEHAVIOUR OF YOUNG: (GFA)

FLEDGING: Young first fly at $c. 6$ months; on Aldabra 169 days (148–202).

POST-FLEDGING: Fed for 6–14 months, probably $c. 6$, but longer not uncommon; more often by female than male. Survival of newly independent young probably varies with area (food) and year, but in Galapagos (1964) many starved (Nelson 1968).

BREEDING SUCCESS: (Galapagos, Nelson 1976; Aldabra, Reville 1980, 1988) Variable; sometimes low but difficult to obtain figures uninfluenced by disturbance. Hatched from laid: 55% (Aldabra 1977). Fledged from hatched: no figures. Fledged from laid: 19% (Galapagos 1964); 51% ($n = 111$, Aldabra 1976); 41% (Aldabra 1976); 53.8% (Aldabra 1977). Survived to independence: 81.8% of fledged young (Aldabra 1977); $c. 10\%$ of eggs laid (Galapagos 1964). Breeding failure due to human disturbance, conspecific interference, starvation and



6.158 Female great frigatebird with chick aged 2–3 weeks.

(some localities) predation of small, unguarded young by (in Galapagos) short-eared owls.

FIDELITY TO COLONY, SITE, AND MATE: Degree of fidelity to colony unknown. Probably returns to same island or island group but unlikely to return to same local cluster as in previous breeding cycle. Neither site nor mate retained in successive breedings. Natal philopatry probably important. Two tagged juveniles returned to within 30 m of natal site 9–12 months after independence i.e. *c.* 2 years old.

AGE OF FIRST BREEDING: Unknown; probably more than 5 years and possibly up to 10.

NON-BREEDING YEARS: Large proportion of colony may be non-breeding; of *c.* 8,500 birds on Aldabra only *c.* 1,800 considered to be breeding.

LONGEVITY AND MORTALITY: (GFA) Breeding life may be 30 years or more (speculation) but biennial breeding and non-breeding years reduces number of fulfilled cycles. Annual adult mortality unknown; probably 5% or considerably less if man excluded.

Lesser Frigatebird *Fregata ariel*

PLATE 11

Atagen ariel G. R. Gray, 1845, no locality given. Raine Island designated by Mathews, 1914.

Other common names: least frigatebird, man o' war hawk. Although 'lesser' leads to confusion with *F. minor* (great frigatebird) so, also, does 'least' and word 'lesser' more commonly used, though *Handbook of Australian, New Zealand and Antarctic Birds* recommends avoiding it.

French: frégate ariel. German: ariel fregattvogel. Spanish: rabihorcado chico.

Sub-species

F. a. ariel Gray 1845 central and E Indian Ocean, Australia, W and SW Pacific. *F. a. iredalei* Mathews W Indian Ocean. *F. a. trinitatis* Miranda-Ribeiro, 1919, S Atlantic Ocean. As with *F. minor*, sub-species of *F. ariel* largely size variants and of doubtful validity. On Aldabra females dimorphic in colour of bill and eye-ring; about two-fifths of population have blue bill and others pink or red.

Description

ADULT M PRE-BREEDING: Almost entirely black with usual frigatebird gloss, here predominantly purple, on head and back. Alar bar said to be lacking but, since it may be present though indistinct in female its absence in male needs confirmation. Black underparts broken (diagnostic) by small, narrow white transverse slot running from mid-body into armpit (several illustrations err on this). Bill dark, iris brown, eye-ring blackish. Crimson gular pouch. Legs, feet reddish.

ADULT F: Head, throat, neck black, like a hood, sometimes reddish on nape. Broad white collar almost meets at back of neck, contiguous with white breast and uppermost abdomen. Black hood extends onto upper breast in sharp 'V' shape. Conspicuous white spur extends from flanks into armpit. Underwing, lower abdomen, vent, undertail black. Upperparts mostly black with broad, buffish alar bar. Bill pink or similar (but see above), eye-ring red. Feet, legs pinkish or red.

POST-NUPTIAL: Little change; male loses sac.

JUVENILE: Head, throat, upper neck reddish brown (deeper than in great frigatebird) mottled when worn. Upperparts black with pale alar bar; broad black pectoral band; white underparts intruding a little onto base of black underwing. Underparts behind legs black. Bill pale grey often with dark tip to upper mandible. Eye-ring pale, or brown. Iris brown. Legs, feet nondescript brownish or flesh. Later, head becomes white variably washed on sides with pale russet. Chin, throat ginger. Breast band disintegrates, belly becomes mottled. From then on gradually acquires adult features. First juvenile plumage lasted over 2 years in captive bird; adult plumage unlikely to be attained in less than 5 years.

Field characters

Adult M readily recognized by combination of all-blackness and white wing spurs. Adult F joins adult female Christmas and to lesser extent female magnificent in white-nuchal-collared appearance with black of head, neck, throat forming hood against

white breast, but white axillary spur of lesser is more extensive than in magnificent but markedly narrower than in Christmas. Also less perfect in shape and doesn't follow curve of wing so much as in Christmas. Smaller than the others, but size deceptive. Rare in Christmas' area and overlaps mostly with great, from which readily distinguishable. Immatures impracticably difficult.

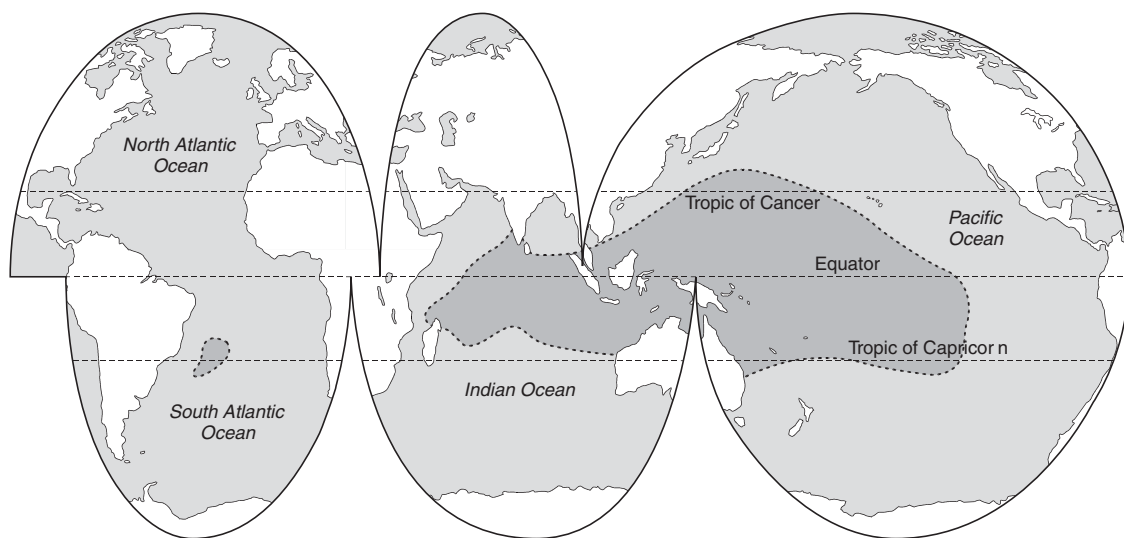
Measurements (see Appendix)

Voice (GFA)

Silent except when landing, displaying or chasing. Male's arrival call a series of short whistles—'weese-weese-weese', female's high-pitched 'chip-ar, chip-ar'. In display males differ markedly from great and Christmas frigatebirds in lacking the warble and using bill-rattle (non-vocal) and a rapid whistle (as above) during gular presentation and during interactions when female lands on display site. Bill-snapping during threat feature of both sexes. Other vocal noises (female only?) include squeals and shrieks.

Range and status (Figure 6.159)

As great frigatebird, Indo-Pacific with Atlantic presence on Trinidad and Martin Vas. Diamond (1975a) analysed distribution of these 2 species: of 21 islands or island groups listed as breeding sites of either, both breed on 10, lesser alone on 5 and great alone on 6. Truly mixed colonies found only on Cocos (North) Keeling, Aldabra (up to 6,000 breeding pairs) and Europa (Madagascar) (1,000–1,200 pairs exhaustively censused and larger than previously supposed, Le Corre and Jouventin 1997b). Commoner than great frigate on Comores (Lovette 1988). Considerable breeding population on Australian Islands (Adele 5,700 nesting pairs, W Lacepede 2,700, Bedout 2,290, all in 1982 Burbridge *et al.* 1987). Breeds on islands of Swain Reefs (up to 100+ pairs on Bell Island). In far northern Great Barrier Reef 'less common' and 'local' (Blaber *et al.* 1998). Widespread Gulf of Carpentaria (greater sparse or uncommon, Blaber and Milton 1994); outer Wellesley Islands support major colonies (Walker 1992). Phoenix Islands (guesstimated 70,000 breeding birds) important



6.159 World distribution of the lesser frigatebird.

stronghold; world's largest colony probably McKean Island with 15,000 pairs (Sibley and Clapp 1967) though estimate now outdated. Enderbury held estimated 75,000 mixed great and lesser in Jan 2000 (A. Kepler personal communication). Baker holds thousands. Though Sibley and Clapp note previously very few records of lessers in central Pacific are in fact abundant S and SW of Johnston Atoll. These authors present details of breeding status on Central Pacific islands (abundant or common 6, uncommon breeder 2, visitor 10). Now only on Christmas Island and Malden in Line Islands (previous estimate 10,000); few or none on Tuamotus and Marquesas (A. Kepler).

MOVEMENTS: Based on recoveries from 4,835 nestlings ringed on Howland and Phoenix Islands, Sibley and Clapp (1967) present a map of probable dispersal routes in relation to prevailing wind patterns (Figure 6.160); follow westerlies from south central Pacific to NE of Australia. 75% recoveries more than 2,000 miles from home island and 31% 6,000–8,000 km (reached New Zealand). 75% recoveries from New Guinea, Bismarck Archipelago, and Solomon and Philippine Islands. Although adults probably do not disperse so far almost all of them reportedly leave their island

during non-laying period (Dec–April) though long breeding cycle means that there cannot be any month during which not some adults with dependent young. Like great frigatebird, and contrary to many statements, lesser not uncommon far (more than 800 km) from land. In Andaman Sea Kiorboe (1991) saw 226 frigatebirds, mainly lesser, in 67 observation hr, chiefly near continental shelf.

Foraging and food (GFA)

Like others. Apparently as pelagic as great frigatebird with which huge overlap in food taken. Analysing regurgitations, Diamond (1975a) could detect differences only when wet season prey and dry season prey analysed separately and even then his interpretation inconclusive. In great frigatebird proportions of *Exocoetus* to *Cypselurus* (flying fish) different in wet as against dry season though proportions of fish to squid remained similar. In lesser, similar changes in proportion of *Exocoetus* and *Cypselurus* but fewer squid and more *Cypselurus* taken in wet season. Moreover, the two frigatebirds took prey of similar size. Whilst this overlap in diet seems surprising in view of size difference and is not what niche-differentiation theory would predict, both frigatebirds are large enough

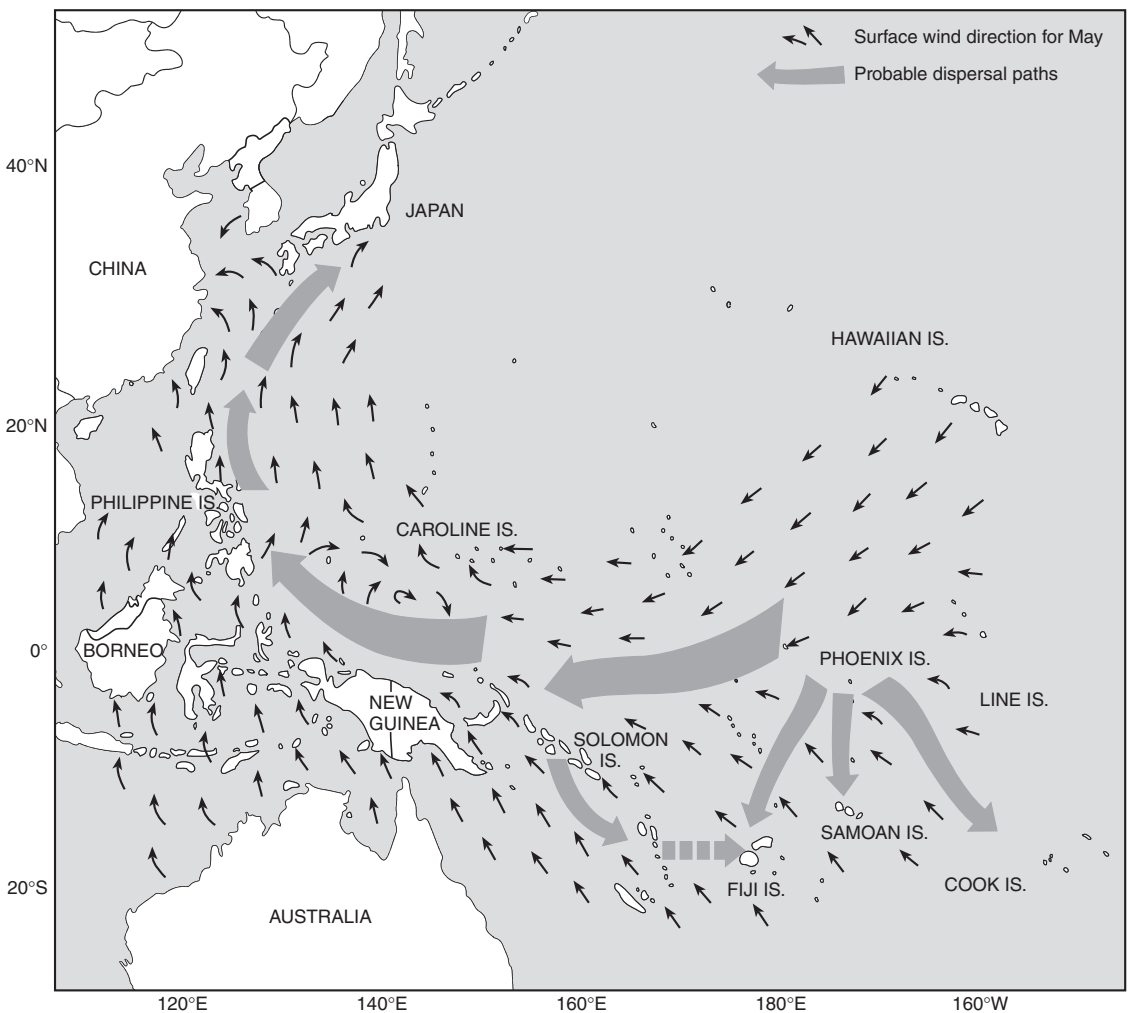
to take all but extremely large items. For kleptoparasitism see GFA. Takes trawler discards (Blaber *et al.* 1995).

Habitat and breeding biology

(See Fig. at end of ch. 5; Sibley and Clapp 1967; Diamond 1975a; Reville 1980, 1991)

HABITAT: Oceanic islands, atolls and low-lying sandy cays even where only sparsely vegetated or

merely shrubby. May be better able than great frigatebird to use such sites. Can rise from ground even under calm conditions and in central Pacific commonly nests there. On Aldabra nests mostly in mid-canopy laterals, like great but also on bushes. Where 2 intermixed, great supplanted many lessers on nests and killed 2 unguarded chicks of 14–21 days before advertising on their nests. On Aldabra lessers substantially changed main nesting locations over a few years, though perhaps due to disturbance.



6.160 Dispersal of lesser frigatebirds in relation to prevailing winds; 28 were >3,000 miles. (After Sibley and Clapp 1967.)

COLONIES: Divided into 'sub-colonies' containing a few score to perhaps more than a thousand nests (120–3,700 cited as sub-colonies on Aldabra) and separated by km rather than m. Within sub-colonies nests unevenly dispersed, usually because of irregular habitat. On Christmas Island (PO) up to 6 nests per bush in *Suriana maritima*. Reville (1991) found that on Aldabra, within groups of 50–150, nests not divisible into discrete clusters but tended towards regular spacing at both high and low densities though often habitat enforced clumping. Diamond (1975a) described them as nesting in clusters of *c.* 20. By contrast great frigatebird nests in more distinctly marked clumps (15–23 commonest) within which nests fairly regularly spaced. Seems to be genuine difference between the two species in spatial pattern correlated with different behaviours during site-selection and display, and one which exerts a significant effect on breeding success. On Aldabra av distance between nests about twice that of great frigatebirds (137 cm against 73 cm).

Colonies contain high proportion non-breeders. On Aldabra total population of great and lesser frigates *c.* 30,000 birds, mostly non-breeders.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Can breed successfully no more than once in 2 years. Breeding cycle occupies *c.* 400 days though probably less on occasion. Presumably, like great, takes 'rest' years. Definitely seasonal though this is protracted and varies with year and locality. Colonies can contain, all at same time, displaying birds, eggs, young birds in nest and dependent but free-flying juveniles from previous cycle. Examples: on Aldabra birds display May–Aug and lay Aug–Nov. Females which eventually laid settled over a period of *c.* 200 days. On Christmas Island (PO) displayed Feb–May and (probably) laid mainly April–May and more synchronized than on Aldabra. In Australia (Queensland) displayed Feb–May and laid March–June. On Raine Island displayed March–June and eggs recorded Feb–Aug with peak in May.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: As others. Apart from specific vocalizations and important differences in spacing of individuals in

display groups and in way such groups subsequently fill up with established pairs (Ch 2), no qualitative differences in physical nature of male's display. Female lesser, however, adopts distinctive 'gooseneck' posture (See Fig. at end of ch. 5) when approaching a display group; not described for any other frigatebird. Seems to be effective in stimulating males to join a group which is being inspected by 'goosenecking' females.

Males occupy sites with old nest platforms in preference to those with no nest-material. They remain there on display for much shorter shifts than in great frigatebird—a few minutes to an hour, compared with up to 6 days. Males do not compete overtly for display-sites. In 556 hours of observation Reville did not once see a male with a sac threaten or attempt to displace another male on a display site but he recorded 200 such instances in great frigatebird. Nor do male lessers use gular-presentation in aggressive male–male encounters though great does. In 'pure' clusters of lessers av 26 days of male advertising (though not necessarily same male) had been expended per nest, in areas of max density. Considerably less than equivalent in great. Nests began to appear almost as soon as males began to advertise whereas in great frigatebird females began to settle in numbers only after males displaying for a month. This produced marked synchrony of breeding in great frigatebird, where females ready to pair 'built up' in numbers. Interference by non-breeding males occurs, as it does in great.

COPULATION: (GFA)

NEST: (GFA) Variably frail platform of twigs. No real cup or lining. Up to 120 pieces nest-material per nest; 60% 2–5 mm diameter and 100–300 mm long (Reville 1980). Nest founded on 2 twigs *c.* 15 cm apart, with 2nd layer diagonally across 1st. Eventually fouled with droppings which may hold twigs together.

EGG/CLUTCH: (Aldabra, Diamond 1975a; others Marchant and Higgins 1990) As others; always one: 60.8×42.1 $n = 8$ Aldabra; $63 (56-72) \times 45(41-8)$ $n = 10$ and $64.5 (58.5-71.2) \times 42.9 (39.6-45.4)$ $n = 6$ Bedout Island; 64×44 $n = 18$ Raine Island. Weight: 59 g but only one in sample, 6.9% female weight.

REPLACEMENT LAYING: Not proven.

INCUBATION: Shared (*c.* 41 days) although on Aldabra females recorded incubating more than males. Shifts variable but shorter than great frigatebird's: Raine Island 2.7 days (8–139 hrs) *n* = 32; Aldabra 3 days (1–6) *n* = 4.

CHICK: Egg-tooth persists *c.* 1 week. Covered in short down except throat and neck, by day 14; scapulars erupt *c.* 21 days; rufous feathers appear on face days 21–5; secondary coverts emerge by day 42 and primary coverts by day 49; secondaries and tail feathers erupt days 56–60 and primaries 60–70. Growth curve Figure 5.40. Sex ratio of young appears to be approx 1:1, unlike that of both great and magnificent.

CARE OF YOUNG: Tended and fed by both parents about equally. After continuous close brooding for 10–14 days chick survival highly dependent on adequate period of guarding. Survivors guarded in total 28 days whereas average at which chicks lost, mainly through attack by unpaired males, was less than this. Difference, though slight, places time of loss towards end of period when successful parents still guarding, when chicks conspicuous and parents had begun to leave them unattended. In 1976 guard period 28 ± 6 days; 1977, 33 ± 7 days, difference probably due to food. Feeding intervals variable but on average young in nest fed approx once per 2 days, mostly in afternoon, but intervals can be much longer (up to 11 days).

BEHAVIOUR OF YOUNG: Begging behaviour as others. Defends perch by striking and gaping. Special temperature control behaviour (GFA). Doesn't sunbathe with upturned wings until free-flying (?).

FLEDGING: No details; first flight must be adequate since would be unable to rise from ground or

(probably) water. Fledge mean 161 days (145–79) *n* = 14 Aldabra.

POST-FLEDGING: Fed for 5–8 months. Growth slower than in great frigatebird; half asymptote of weight and bill length takes about twice as long. Fledged but dependent young fed less frequently than those in nest and spend most of time away from colony which they leave *c.* 5–12 months after fledging.

BREEDING SUCCESS: (Reville 1980, 1991) Hatched from laid: 22.8% (*n* = 136, Aldabra 1976); 17.4% (*n* = 161, Aldabra 1977). Fledged from hatched: 48% (Aldabra 1976), 75% (Aldabra 1977). Fledged from laid: 10–15% (Phoenix 1963, Sibley and Clapp 1967); 11% (Aldabra 1976); 13% (Aldabra 1977). Survival to independence: no figures. Extremely low success, Aldabra, substantially due to nest-usurpation, including killing of nestlings by conspecifics. It emphasizes significance of this phenomenon in frigatebird breeding biology though effect of observer-interference in facilitating such attacks must not be ignored. Interference greatest in areas of high nesting density. Reville (1988) links greater success of great frigatebirds to greater synchrony.

FIDELITY TO COLONY, SITE, AND MATE: Like its congeners, does not retain site and mate in successive breedings. Degree of fidelity to colony not known.

AGE OF FIRST BREEDING: Thought to be at least 7 years.

NON-BREEDING YEARS: No information but likely to occur.

LONGEVITY AND MORTALITY: No specific information, but see GFA.

Tropicbirds

Red-billed Tropicbird *Phaethon aethereus*

PLATE 12

Phaethon aethereus Linnaeus, 1758, Ascension Island.

Other common names: white-tailed bos'n bird, longtail, marlin spike.

French: phaeton à bec rouge, paille-en-queue éthérée. German: rotschnabel-tropikvogel. Spanish: rabijunco etereo, rabijunco comun.

Sub-species

P. a. aethereus S Atlantic. *P. a. mesonauta* E Pacific, E Atlantic and Caribbean.

P. a. indicus Persian Gulf, Gulf of Aden, Red Sea, Arabian Sea, E to Gulf of Oman and E Arabian Gulf.

Description

ADULT M PRE-BREEDING: Mainly silky white, may be suffused with variable amounts pink. Conspicuously black wing-tips on upper surface due to black outer four primaries and their coverts and some black on inner secondaries. Underwing white. Large patch of blackish vermiculations on back extends onto upper tail. Black eyestripe may continue onto nape but much reduced or absent in Red Sea-Indian Ocean. Underparts white with some grey on flanks. Long white tail streamers with black shafts. Bill stout and red, iris dark brown. Legs pale, webs black. On Ascension feet varied from pale pink to chrome yellow.

ADULT F: Similar.

POST-NUPTIAL: Little change.

JUVENILE AND IMMATURE: Heavy black barring on upperparts, dark grey bars on crown, nape, hind-neck. Bill yellowish/orange becoming red within first year. Immature separable from adult for 2–3 years on plumage as barring diminishes.

Field characters

Differs from other species in combination of red bill, white streamers, and narrow black barring on back. Size difference between this and red-tailed little use in field though latter more heavily built, blunter-winged, and appears all white. White-tailed smaller with broad, black, diagonal wing-bar and yellow bill. When soaring, red-billed, unlike red-tailed, usually reveals barring on inner secondaries of underwing. Tropical Atlantic race may be strongly pink, Red Sea race has more orange bill and less (or no) eyestripe. Barring on juvenile's upperparts finer and denser than white-tailed; black on nape more distinct.

Measurements (see Appendix)

Moult (GFA)

Post-nuptial moult (Ascension) took 24 (19–29) weeks (Stonehouse 1962).

Voice

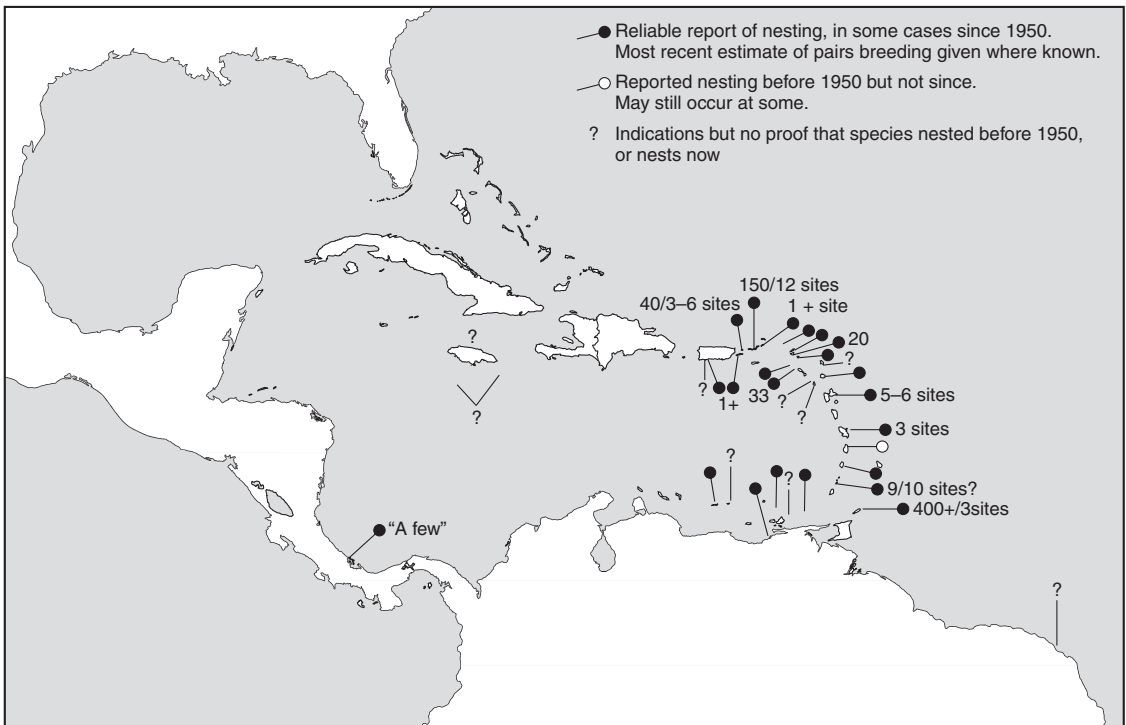
Shrill whistle at sea definite for this species though questioned for others. At breeding colony screams, screeches, cackles during display, territorial disputes

and when disturbed. Screams during display completely distinct from 'chuckle' of white-tailed. Not recorded to growl like red-tailed. Clicks and guttural chucks by adult when feeding young. Alarmed young give piercing, pulsing, protracted scream.

Range and status (Figure 6.161)

Tropical and sub-tropical seas; probably least numerous of tropicbirds. World population guessed at fewer than 10,000 pairs. Major concentrations in Caribbean *c.* 1,500 or more pairs, confined almost entirely to eastern sector. Most numerous Tobago and Virgin Islands though occurs from Puerto Rico to St. Vincent (van Halewyn and Norton 1984). *Locus typicus* S Atlantic population in serious decline; only small numbers Brazil and Cape Verde Islands; even in 1969 de Naurois estimated fewer than 1,000 pairs and declining. Occurs Razo, Rhombos (persecuted), Sao Tiago, Boa Vista, possibly Sao Antao. On Ascension (Bosun Bird Island) *c.* 500 pairs. Breeds Fernando Noronha and St. Helena.

Recently recorded breeding in Azores (Furness and Monteiro 1995). Current 4 localities in S Atlantic probably fewer than 3,000 pairs. Annobon, Sao Tome, Principe hold both red-billed and white-tailed but probably not in large numbers; subject to exploitation. Breeds in Arabian and Red Seas and Gulf of Aden. Off Ethiopia breeds in Dahlak archipelago and, off Somalia, on Mait Island (Cooper *et al.* 1984) probably in small numbers. Noted Gulf of Suez. Apparently breeds on Socotra and Abd-el-Kuri, S Yemen (Cooper *et al.*), commonly on rocky islands and mainland coastal cliffs, certainly from Halul Island eastwards in Arabian Gulf, around coasts of Arabia (Gallagher *et al.* 1984). Common on Mekran coast though not proved to breed; occurs Pasmī to Omarra most months. Probably widespread in Red Sea. Nests on Kuria Murias (Al Hallaniyah, Al Qibliyah). In south central Arabian Gulf nests on Arzanah, Qarnayn, Zarka, Sir Abu Na'ayr. Recorded Bay of Bengal and (inadequate evidence) South China Sea; status



6.161 Breeding distribution of the red-billed tropicbird in the Caribbean (1,600+ pairs). (From Halewyn and Norton 1984.)

obscure. In Pacific occurs in E from Gulf of California S to San Lorenzo Island where breeds. Probably c. 100 pairs breed in Revillagigedos. On San Benedicto possible that both red-tailed and red-billed breed—rare phenomenon. Former not proved to breed but 1988 one or two pairs displaying. Recently recorded courting and landing Santa Catalina, Costa Rica (Duffy and Hoch 1995). Galapagos (no white-tailed) hold possibly several thousand pairs—e.g. c. 450 pairs on Daphne. Chile southernmost nesting place on uninhabited Chanaral (29°02'S, 71°37'W) (Vilina *et al.* 1994) and first breeding record for Sala y Gomez island (Vilina and Gazitua 1999). Rare in central and W Pacific. Overlaps with red-tailed in central Indian Ocean only.

MOVEMENTS: Outwith breeding dispersive and resident. Some adults near colonies throughout year. Galapagos adults may move at least 1,500 km. Ringed adult from Galapagos caught off Peru so this population may disperse widely in E Pacific. Possible dispersal of populations from Senegal to Guinea Bissau to upwellings off W Africa. Some from Caribbean go to W Sargasso Sea. Disperses into Gulf of Suez, Red Sea, Arabian Sea, Persian Gulf (Cramp and Simmons 1977). Seen off Costa Rica, Israel and Pakistan (del Hoyo *et al.* 1992). Occurred W India, Laccadives, Bay of Bengal, off Madagascar. As in other tropicbirds juveniles probably go further than adults and consequently form bulk of vagrancy records.

Foraging and food (GFA)

Solitary; only one tropicbird in 134 feeding flocks in NE tropical Pacific (Au and Pitman 1986). Possibly, different colonies utilize specific feeding areas (see white-tailed for energetic considerations). Thus, in Galapagos evidence that in some colonies (but, significantly, not all) periodic severe food shortages leading to desertion. On Plaza (Galapagos) adults spent more time with chick (Snow 1965) than on Ascension (Stonehouse 1962) and Plaza chicks healthy even in years when some Galapagos populations obviously short of food.

On Ascension small (10–20 cm) regurgitations contained flying fish *Exocoetus volitans*,

Oxyporhamphus micropterus, *Ophioblennius webbii* and *Halocentrus ascensionis*. Larger (>25 cm) *Cypselurus* and *Hirundichthys*. In Galapagos fish up to 20 cm given to chick. Also takes squid *Hyaloteuthis pelagicus* especially in some regions—e.g. Indian Ocean.

Habitat and breeding biology

(See Fig. at end of ch. 5)

HABITAT: Prefers holes in cliffs or beneath or among rocks or laval crust on oceanic islands but will nest on open cliff-ledges or among vegetation.

COLONIES: Never large, usually moderate (<1000 pairs), often small. Dispersion variable depending on available sites. Solitary or well dispersed in small groups but may nest within metre of neighbours.

FREQUENCY, TIMING, AND DURATION OF BREEDING: On Ascension bred at intervals of 9–12 months. Successful breeders laid at intervals of 306–58 days $n=13$, unsuccessful after egg-loss at 259–336 days $n=7$, unsuccessful after chick-loss at 294–357 days $n=6$ (Stonehouse 1962). In Galapagos, on some islands e.g. South Plaza (Snow 1965, Harris 1969) successful cycles at 12-month intervals with no out-of-season nesting whilst on others possibly at less than that and eggs laid in all months. On Tower most laid June–Aug with considerable synchrony, though eggs in every month (Harris 1969). On Daphne many birds returned to breed 3–4 months after losing egg or chick. Overall, seems unlikely that successful pairs breed more often than once per 11–12 months. Acquisition of territory and courtship takes at least 3–5 weeks. Harris notes that on South Plaza adults frequent site and display for at least 2 months before laying. Laying and incubation takes 6 weeks, care of young 12–16 weeks, dispersal and moult 19–29 weeks, midpoint c. 50 weeks.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Territorial and courtship behaviour occupied 4–6 weeks, Ascension; may involve intense fighting and threat in competition for hole-sites (Stonehouse 1962). Intraspecific strife may affect entire breeding phenology. Thus on Daphne (Galapagos) Snow (1965) found nesting almost continuous, with more

pairs than nest-sites giving rise to intense competition, disruption, and turnover of nest-sites contributing to low breeding success. Yet on nearby Plaza nesting seasonal (though well extended), more sites than pairs, less disruption, and higher success.

Aerial courtship noisy and communal (GFA), birds joining and leaving display groups. Flight mazy, with wheeling, climbing and descending in long glides, also zig-zagging, changing direction every few wing beats like some terns. Streamers switched from side to side, birds call loudly. No detailed analysis available.

COPULATION: (GFA)

NEST: (GFA) Simple scrape; some adventitious material.

EGG/CLUTCH: (Ascension—Stonehouse 1962; Galapagos—Harris 1969). Always one; ovoid, matt, whitish-buff background with dark-brown or reddish marks or blotches: 59.06×42.10 $n=20$ various localities; $64.5 (55-76) \times 45 (33-50)$ $n=245$ Ascension; 59.9×42.7 $n=6$ Galapagos. Weight: 67 (32–84) $n=32$ Ascension; 58.2 (51–64) $n=7$ Galapagos, comprising 8–9% of female's weight. Galapagos eggs significantly smaller than Ascension. Daily weight loss of 0.20 g $n=11$. Monthly volumes of eggs did not

differ (Ascension). Yolk 18 g, albumen 33.5 g, shell 5.5 g.

REPLACEMENT LAYING: After egg-loss, Ascension, mean interval 41.5 weeks (37–48) $n=7$ accurately known. Rarely without intervening moult. Some birds remained at nest several months after loss. Loss of chicks (6 cases, 4–10 weeks old) followed by laying 46 weeks (42–51) after laying of first egg.

INCUBATION: (GFA) 42–4 days. Shifts (Galapagos) longer than 6 days but likely to be extremely variable (see red-tailed).

CHICK: Hatchling *c.* 36 g. Born with thick white down except base of bill and lores. Tinged grey-fawn on back. Close brooded at first; in Galapagos one adult normally remained with chick until at least two-thirds grown.

Feeds (vomited) 30–50 g (chick 11–20 days), av 85 g (21–30) though 25 day-old received 120 g. Chicks 31–50 days av 130 g. Largest 180 g (45 day-old).

Scapulars erupt day 13, secondaries 22, primaries 24–7 and tail feathers 30–5. Down clears rapidly 40–5; little remains after 55. At day 2–3 indistinguishable from white-tailed at day 6–7.

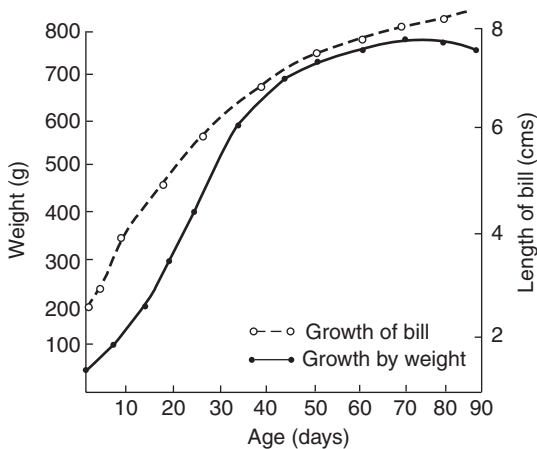
CARE OF YOUNG: (GFA) Shared; attendance gradually waned. On Ascension adult present 82% observer visits (chicks 0–5 days) to 10% (chicks 61–70); little thereafter. In Galapagos adults found with chicks up to 50 days in 93 of 112 checks compared with only 227 of 429 checks on Ascension. At first fed daily; from day 70 once per 2–3 days (Ascension).

BEHAVIOUR OF YOUNG: (GFA)

FLEDGING: (GFA) First fly Ascension 83–104 days, mainly 80–90; Galapagos 79, 86, 84 ± 3 , 87 ± 1 , 90 ± 3 . Galapagos chicks fed up to fledging (Harris 1969).

POST-FLEDGING: (GFA)

BREEDING SUCCESS: Hatched from laid: 69.2% ($n=328$ Ascension). Most losses due to competition



6.162 Growth of the red-billed tropicbird (Atlantic). (After Stonehouse 1962.)

for sites; on Plaza 10 out of 19 lost through intra-specific fighting often early in breeding cycle (Harris 1969) despite low density of nests. Fledged from hatched: 82.3% (Ascension). Fledged from laid (highly variable): 32% (Daphne, Galapagos); 44% and 55% (Plaza, Galapagos); 51.5% (Ascension). No evidence for starvation on Ascension but may occur in Galapagos where Harris (1969) found many dead young on Tower Island, at a time, moreover, when this species breeding successfully on Plaza. Many had left their burrows and died on the lava whilst others had flown prematurely and drowned. One dead youngster near fledging age weighed 320 g, *c.* 50% normal fledging weight. Some predation by short-eared owl in Galapagos; a few deaths due to frigatebirds chasing fledglings. Apparently, unlike many seabirds, believed not to be much affected by black and brown rats, present on even remote seabird islands in Caribbean, though white-tailed not equally immune. On Ascension considerable competition between this species and white-tailed profoundly affects breeding success. Presumably smaller white-tailed suffers more. In Galapagos, intra-specific competition significant cause of failure.

FIDELITY TO COLONY, SITE, AND MATE: Circumstantial evidence indicates high degree of fidelity

to colony. Where little intra-inter-specific competition for sites (little disruption of breeding cycles) site-mate fidelity likely to be high. Ringed birds usually recovered where ringed, or nearby. But notable exceptions as on Daphne where different adults usually involved in successive nestings in same hole (Snow 1965).

AGE OF FIRST BREEDING: Not certainly known but likely 2–3 years. Galapagos chick caught as non-breeder in 4th year whilst 2 other 4th-year birds breeding, probably for first time (though not certain) and 2 in 6th year (Harris 1979b).

NON-BREEDING YEARS: No details, but likely.

LONGEVITY AND MORTALITY: Of 51 breeding adults ringed Galapagos 1965–70, at least 82.3% survived at least one year (Harris 1979b) which, with possible emigration, non-breeding and ring-loss suggests annual adult mortality of less than 10%. No information on pre-breeding mortality but, assuming no post-fledging feeding, sometimes-impooverished, blue-water feeding zones and difficult (plunge-diving) method of feeding, likely to be high, further indication that adult mortality must be low if populations to remain stable.

Red-tailed Tropicbird *Phaethon rubricauda*

PLATE 12

Phaeton (sic) *rubricauda* Boddaert, 1783, Mauritius.

Other common names: silver bosunbird, strawtail. French: phaeton à brins rouges. German: rotschwanz-tropikvogel. Spanish: rabijunco colirrojo (cola roja).

Sub-species

Although Peters (1931) originally recognized 4 sub-species they probably form a north-south cline. *P. r. rubricauda*, W Indian Ocean; *P. r. westralis*, E Indian Ocean; *P. r. roseotricta*, SW Pacific; *P. r. melanorhynchus*, W, central and S Pacific. Criteria for separation are slight differences in size, including eggs. Rosy tinge, though used as criterion,

is seasonal. Measurements clinal, increasing between Kure Atoll in N Pacific and Kermadec Island in S. Tarburton (1989): 'the illusion that birds from this cline comprise three sub-species has long been accepted because the large range of latitude that each subspecies has been arbitrarily given resulted in significant differences in mean measurements' i.e. continuum of samples rather than disjunct ones would reveal the cline.

Description

ADULT M PRE-BREEDING: Especially silvery-white, often pinkish. Black shafts to outer primaries, conspicuously black on tertials. Dark eye accentuated by black eyebrow extending down in front of and

a little behind eye. Dark streaks flanks, axillaries; otherwise white below. Long red central tail streamers. Stout red bill, grey-black around open nostrils. Webs, toes black distal two-thirds, pale bluish proximally.

ADULT F: Similar.

POST-NUPTIAL: Little change.

JUVENILE AND IMMATURE: Entire upperparts heavily barred blackish, upper primary coverts black and white, black on crown, nape, lores. Bill blackish. Tail black-tipped, lacking streamers. Over 2 or 3 years black decreases as adult plumage gained. Sub-adults still retain heavy speckling on dorsum. Adult plumage can be attained two years after hatching. However the (few) birds which returned to Johnston (PO) at 9 months had adult plumage except for some black spots on scapulars (Schreiber and Schreiber 1993).

Field characters

High flight often obscures markings. Adult's red streamers diagnostic but red bill shared with *P. aethereus*. Appears stockier and shorter or more rounded-winged than other tropicbirds. Immatures have dark or reddish bill, not part-yellow as in *P. lepturus*. Could be impossible to distinguish from immature *aethereus* but range does not usually overlap.

Measurements (see Appendix)

Voice

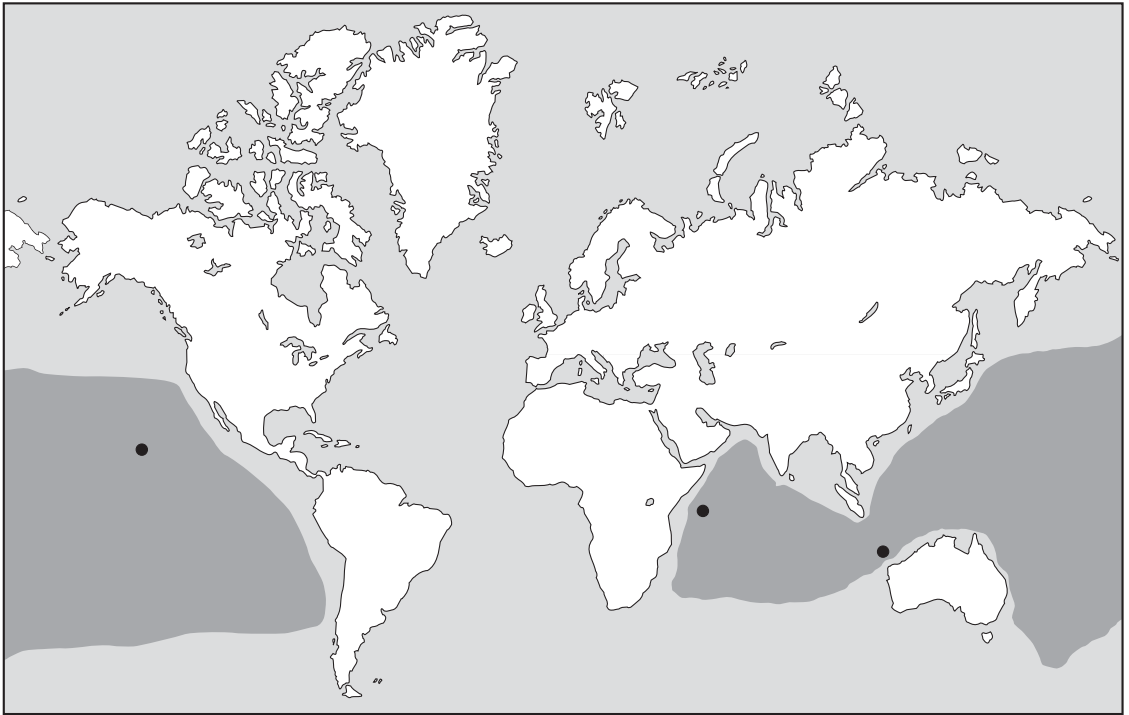
Silent at sea. Whistle needs confirmation. In breeding area calls during flight display 'ee-yip' repeated. Also cackles and croaks. Soft contact note between mates; long, loud ratchet growl or snarl on ground when aggressive towards non-specifics (responds to tape of this call by exact repetition). Also screeches in defence. No vocalization recorded when feeding young. Chicks at first beg with soft 'eh-eh-eh' but by 2–3 weeks squawk like adults though less strident.

Range and status (Figure 5.41; 6.163)

Solitary and pelagic, e.g. one bird per 1,600 km diurnal observation (King 1970). Occurs

characteristically in trade wind areas of central and W Pacific and S Indian Oceans mainly to *c.* 30° N and S but straying well outside those limits; recorded at 42° S (King 1974). N of equator recorded at higher latitudes in far W Pacific (30–5° N) than in far E (20–5° N) probably because warm water currents go further N in W Pacific. Seasonal northward movement of central gyre waters enables it to breed in temperate latitude of Midway Island (28°13' N). May breed San Benedicto and Clipperton. In eastern S Pacific breeds on Henderson Island (24°22' S, 128°18' E). Breeds Cook Islands, especially Takutea, now protected. Occasionally occurs New Zealand (nests on Kermadec Islands)—8 beached records up to 1993 though 18 reports of birds seen around New Zealand N to Three Kings Islands, mostly after northerly gales. Breeding recorded Houtman Abrolhos (28°46' S, 113°58' E) in 1940s–1950s. Displaying 1990 (Fuller and Burbridge 1992).

Rough estimates of some populations: *c.* 12,000 pairs Hawaii—largest Midway *c.* 5,000 pairs (Fefer *et al.* 1984); Kure 1,000–1,100 nests (2,500 birds max); also large colonies on Laysan and Lisianski (Schreiber and Schreiber 1993). Harrison *et al.* (1984a) say on main Hawaiian islands nests scattered in small numbers except on Kahoolawe, Lehua, Kaula. 'Historical records for Nihoa and Lisianski indicate no conclusive changes over time. . . recent populations are apparently stable throughout northwest Hawaiian Islands but Johnston population seems to be increasing'. In late 1960s population of Pacific guessed at >31,000 birds (Gould *et al.* 1974) but A. Kepler (personal communication) says huge decline since then. Christmas Island (PO) decreased from 3,000 pairs to fewer than 1,000 pairs in 1991 due to human persecution (Schreiber and Schreiber 1993). Known from at least 9 groups of islands in S Pacific. Reported breeding Caroline Atoll 1990 (Kepler *et al.* 1994). Indian Ocean: *c.* 2,000 pairs Aldabra, query for Glorioso, fewer than 100 pairs in Seychelles, more than 100 pairs Mascarenes, not known to breed Laccadives, Maldives, Chagos, Andamans, Nicobars. Fewer than 100 pairs Cocos Keeling (Feare 1984), 1,300+ pairs Christmas Island, 3,000–4,000 pairs Europa (Madagascar) (Le Corre and Jouventin 1997b), several thousand Indonesia and Banda Sea.



6.163 Marine range of the red-tailed tropicbird with three breeding localities indicating its wide distribution. (After Schreiber and Schreiber 1993.)

Along with white-tailed, not recorded in Melville's (1984) account of seabirds of China and surrounding seas.

World population (only moderate) variably estimated to be about stable or more likely declining. Like other seabirds, locally and temporarily affected by major perturbations such as El Niño in Pacific, permanently by poaching and feral cats.

Overlaps with red-billed in Central Indian Ocean and with white-tailed extensively in Indian and Pacific.

MOVEMENTS: Outwith breeding, widely dispersive, thousands of km. Apparently, birds from N of equator usually do not cross equator, possibly (Gould *et al.* 1974) because food-rich equatorial counter-current acts as limit. Birds from N Pacific appear to disperse in easterly direction, central Pacific birds in westerly, both following prevailing winds (Schreiber and Schreiber 1993). Very occasionally offshore E Australia. East-west from

c. 500 km off W coast of Americas to SE Australia, Taiwan, and Japan. Occasional inland, presumably wind-driven.

Foraging and food (GFA)

More pelagic than other tropicbirds. Warm, salty waters of surface temperature 24–30°C. In Pacific, boundary set by summer surface water isotherm of 22°C. Avoids water of less than 33.5 parts salt per 100,000 in N hemisphere and 35 parts in S (Gould *et al.* 1974). Changes in surface temperature and salinity may affect breeding range, as apparently off W Australia where southward extension has accompanied rise in temperature (Dunlop and Wooller 1986). Upwellings and local divergences increase nutrients and provide richer feeding areas in impoverished tropical seas. Usually feeds singly; sometimes with e.g. sooty terns or shearwaters (Gould *et al.* 1974). Exploits mainly first 4 m of water column (mean max depth of dives 4.6 ± 2.7 (1–13 m) (Le Corre and Jouventin 1997a). They found birds from Europa

(IO) caught mainly squid (51.5%), dolphins *Coryphoenidae* 14.9% and flying fish *Exocoetidae*. Rarely, catches latter on wing. In Hawaii samples contained 24 species of fish, 2 families of squid (82% fish, 18% squid by volume Harrison *et al.* 1983). Christmas Island (IO) fish constitute *c.* 80% mass of diet, squid 20% (Stokes 1988). Christmas Island (PO) fish only 53%, squid (mainly *Ommastrephidae*) 47% (Ashmole and Ashmole 1967). Takes fish up to at least 22 cm. Frequently harassed by frigatebirds.

Habitat and breeding biology

(See Fig. at end of ch. 5; Fleet 1974; Diamond 1975b; Stokes 1988; Tyler 1991; Schreiber 1992, 1994; Schreiber and Schreiber 1993)

HABITAT: Oceanic islands, volcanic stacks, atolls and cays from sea level to 250 m and, rarely, on mainland. Prefers coastal cliffs, where nests in holes and crevices but also on ledges, among boulders, among or beneath vegetation (on atolls breeds beneath evergreen shrubs e.g. *Tournefortia argentea* and *Scaevola sericea*) and will even nest on low-lying and flat ground. If among vegetation crawls to clear take-off space. For quantification of site types on Aldabra see Diamond (1975b). On Christmas Island (IO) nests are on bare inland cliff-faces regardless of exposure; avoids rugged, exposed sea-cliffs, which catch ocean swell (Stokes 1988) though will nest on sheltered sea-cliffs (personal observation). Usually seeks shade or overhang but can tolerate open sites. Reluctant to fly under tree canopy.

COLONIES: Usually small (<1000 pairs) to moderate (up to *c.* 5,000 pairs) but depends on definition of 'colony'. Nests usually solitary or well-dispersed in small groups. On Midway, in clumps of *Scaevola*, av nearest-neighbour distance *c.* 169 cm and slightly less along lagoon beach (Woodward 1972) but occasionally adjacent nests much nearer.

Colonies may contain substantial numbers of non-breeders flying over island or roosting in potential breeding areas.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Approx annual breeder with greatly

extended but fundamentally seasonal regime. Over long enough period laying peaks may fall in any month. For instance on different parts of Christmas Island (IO) different groups may show laying peaks at different times of same year apparently depending on exposure to prevailing weather (Stokes 1988). He recorded egg-laying from Nov–July (mainly Feb–May) last replacement eggs laid Aug. On Aldabra pronounced peaks, troughs, and considerable group-synchrony. Over 20 months 2 pronounced peaks and troughs corresponded with onset of driest months *contra* white-tailed (Prysjones and Peet 1980). On Midway, one of most northerly stations, nesting (most eggs March–June) coincided with summer, avoiding cooler-water period (Tyler 1991, 1996). In 1988 21% of annual total laid latter half of March; 2nd peak, last 3 weeks May, produced 22%. But 1989 no March peak; 65.4% laid May or later, laying more synchronized. In Pacific, during ENSO, may not even try to nest, may delay breeding or experience total failure (Schreiber and Schreiber 1993).

Requires 5–6 months for complete breeding cycle. Period between first seen at nest-site and subsequent laying highly variable, av *c.* 40 days. On Kure territory established and defended up to 3 months before laying (Fleet 1974). Schreiber and Schreiber (1993) record 3 cases of new eggs on site where no adult previously even seen. Successful breeding no more than once a year.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: (GFA) Occasional fatalities in prolonged fighting for sites. Communal aerial courtship (See Fig. at end of ch. 5) may involve up to 20 birds—usually 2–15 (Schreiber and Schreiber 1993). Characterized by 'back-pedalling' flight up to 100 m high. Group describes wide, slow circles into wind, calling 'ee-yip' or 'ki-yek' with emphasis on second syllable. Uppermost bird tilts upwards and beats wings rapidly, moving upwards and backwards. At peak ascent remains stationary, switching tail streamers to one side. Then tips forwards and glides under second bird who then begins hover upwards-and-backwards before, in its turn, gliding under first. 2–3 may leave group and glide down with wings held stiffly above body, to

within few m of ground or water. Courtship accompanied by croaks and cackles as well as 'yip' call. Fleet (1974) notes even established pairs may spend *c.* 45 days (up to 91) in pre-laying activities but this period includes long absences at sea and Schreiber and Schreiber emphasize important saving in energy and time at colony by maintaining previous year's mate. Of 76 colour-coded birds displaying over a 7-day period *none* was nest owner. Individuals participated 2–5 days, disappeared for several days, returned, and displayed again. Continuous turnover in displaying group. Most courting birds 2 years old; probably not previously mated. Partners with previous experience may quickly lay after return (Schreiber and Schreiber 1993).

COPULATION: (GFA)

NEST: (GFA) On ground, under vegetation, or in crack or hole in cliff. Either egg on bare substrate or on scraps in shallow scrape, but full grass lining recorded. Scrape 4–10 cm deep, 12–20 cm across. Mostly within 1 m (but up to 6 m) from edge of bush. Av distance between nests 1.5 m (Fleet 1974).

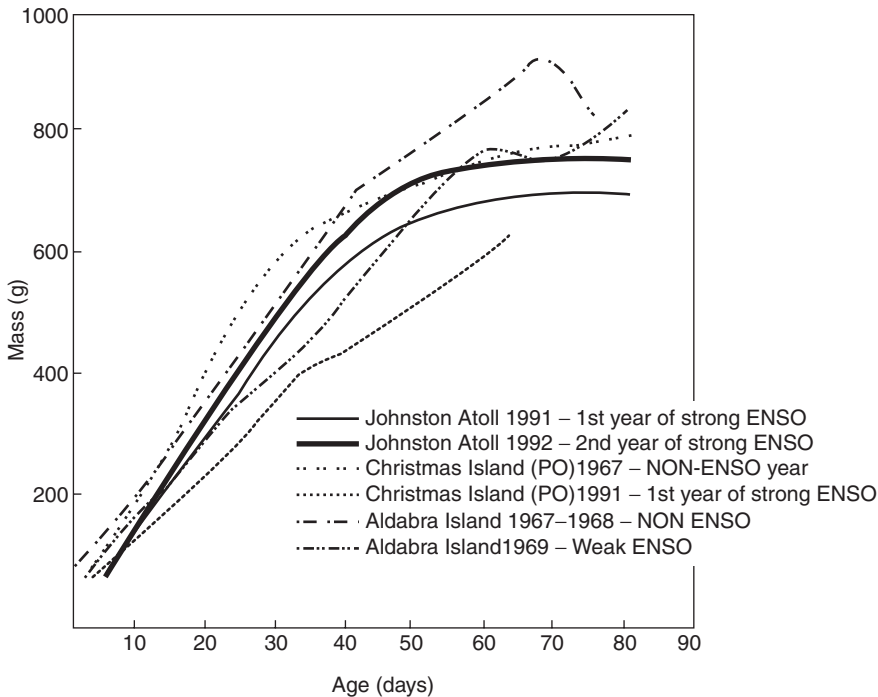
EGG/CLUTCH: Rare 2-egg clutches—e.g. 1 in 8,000 (Schreiber and Schreiber 1993)—probably two females. Egg ovoid to pyriform; fawn with brown or purplish spots larger and denser at broader end. Johnston $64.3 \pm 0.15 \times 44.9 \pm 0.08$ $n = 367$. Shell thickness pre-1947 2.00 ± 0.19 mm; 1965–68 1.92 ± 0.18 (Morrison 1979). Christmas Island (IO) 64.9 (54.8 – 72.2) \times 45.7 (41.1 – 48.8) $n = 113$. Norfolk Island 67.7 (62.7 – 74.2) \times 47.7 (42.2 – 49.9) $n = 23$; 67.3 (59.9 – 73.6) \times 48.1 (45.8 – 50.1) $n = 16$. Raine Island 63.9 (54 – 77) \times 44.9 (40.6 – 49.9). Weight: Johnston 66.8 ± 0.35 $n = 367$. Aldabra 77.4 (SD 7.2) $n = 10$, shell 75 g. Christmas Island (PO) 71.1 ± 0.35 ; Christmas Island (IO) 75 (62.5 – 88.0) $n = 29$. 77.4 $n = 10$; 71.56 $n = 11$. Egg *c.* 9.8% female weight, smaller in N part of Pacific range, larger in S. Water loss during incubation 12.9% of fresh egg; 17.1% occurs between starring and hatching, which may take >93 hours (Whittow and Grant 1985).

REPLACEMENT LAYING: (Midway, Tyler 1991; Aldabra, Diamond 1975b) Common. Defined as laying within 2m of failed site and involving at least one recognizable individual. On Midway accounted for 12–13% of May eggs, 21–7% June–July eggs. Replacement layings decreased as season advanced (80% were replacing eggs laid before end April); 20–35% of such birds re-laid against 5–13% if 1st egg laid in May. 15–20% failed nesters re-laid after mean interval of 33 days (21–58). On Aldabra took 40–71 days; Christmas Island (IO) *c.* 4–5 weeks (Stokes 1988). Birds failing in 1st month of chick stage may also re-lay but no pair which had spent more than 10 weeks on first attempt re-nested (on Christmas Island late chicks less successful than early). Mean volume 2nd egg 4.79% less than 1st (Fleet 1974).

INCUBATION: (GFA) Usually 42–5 days. Kure 43.8. Johnston 42.7 (39–45) $n = 63$. Midway 42.4 ± 1.1 $n = 183$. Aldabra up to 51. Period 47% longer than predicted by egg-mass; low rate water loss due to fewer shell pores. Not significantly different for replacement eggs. Egg can withstand up to 5 days non-attendance (presumably only in shade). Shifts (both parents) variable; Kure 8.12 days (4–16). Johnston 6.3 (3–9). Midway 8.4 (4–13) $n = 293$ excluding first shift of female, often <1 day, rarely >3 (av length declined from *c.* 10 days in March to *c.* 7 in July). Christmas Island (PO) 10.4 (7–12) (possibly longer than usual due to ENSO). Incubation temperature 37°C (Howell and Bartholomew 1962); egg temperature 36.35° (Whittow and Grant 1985).

Egg fractures 3–5 days before chick emerges. Incubating birds lose 30–40 g (day 1); 20–5 (days 2,3), 13–16 thereafter (Schreiber and Schreiber 1993) but some take short excursions (1–2 hours) and feed (weight increases).

CHICK: Hatchling *c.* 48 g, culmen 12–15 mm, wing 16–23, tarsus 12–19; (unattended (in shade) able to maintain body temperature at 38.4–39.2°C (Howell and Bartholomew 1962). Eyes brown, fully open *c.* 2 days but chick at first very inactive. Egg tooth may persist to 6 weeks. Bill grey with black tip, gape pale grey. Bare skin blackish. Legs, feet grey, webs grey and black. Covered grey or



6.164 Growth by weight of the red-tailed tropicbird in various nesting areas and in ENSO and non-ENSO years. (From Schreiber and Schreiber 1993, Aldabra data Diamond 1975.)

whitish down 10–15 mm long, thicker and more upstanding on back, head, sparse on lores. Grey by time feathers erupt.

Precise pattern of growth dependent on food supply; hence differs between localities and may also reflect the severity of ENSO events, which much retards growth (Figure 6.164; Schreiber and Schreiber 1993; Schreiber 1994). On Johnston, where effects felt only during first year of the event (1991), wing growth slow at first but increases after 10 days levelling off at 35 days; max rate of growth 5 mm per day. But on Christmas Island (PO) growth severely retarded. On Aldabra (IO) growth markedly poor in 1969 (although ENSO only weak) compared with 1967–68, a normal year.

Culmen, tarsus, foot grow fastest during first third to half of fledging period. Scapulars erupt 9–17 days, secondaries, tertiaries 14–21 days, primaries, rectrices 21–7 days, tail feathers visible *c.* 30 days. Down disappears *c.* 11 weeks except for patches among coverts, on lower breast, belly, flanks; rump last to clear. Weight peaks *c.* 650–750 g and

then fluctuates. Max weight (Kure) 115–28% adult weight but most excess lost 4–8 days before fledging at which weighs 680.2 g (cf. ad 611.6 g). At fledging (Kure) culmen 58.01 (cf. ad 62.69), wing 300.4 (cf. 320.1), tarsus 29.2 (as adult). Johnston wing length 304–25 mm (cf. ad 328); weight 719 g ± 7.10 *n* = 50–*c.* 110% ad (659 ± 2.93 *n* = 411) but some chicks weighed several days before fledging and would lose weight. Aldabra max chick weight 115% of adult. Parents of large chicks absent from colony >23 hours per day. Feed can be 60–140 g (up to 22% adult weight). Surprisingly, doubling-up chicks showed that parents can raise both by increasing frequency and weight of feeds; no data on survival of these twins (Schreiber and Schreiber 1993).

CARE OF YOUNG: (GFA) On Aldabra av 1.4 feeds per day mostly around midday, occasionally at night (Diamond 1975b). On Christmas Island (PO) 0.9 feeds per day and on Johnston 1.3 (Schreiber 1994). Give 1–5 transfers of food per feeding bout.

Most feeds 10.00–14.00 hr (PO). Will feed substituted chick(s); can increase provisioning to cope with two (Schreiber and Schreiber 1993). Experimental manipulation of food requirements of chick and parental response (Schreiber *et al.* 1996) showed that even during ENSO adults tailored supply appropriately to demand. However, (Schreiber 1994) provisioning rates did differ among ENSO years; in some, chicks were fed fewer and smaller meals and growth (mass) reduced. But chicks did not undergo much fasting.

BEHAVIOUR OF YOUNG: (GFA) Movements of hatchling uncoordinated but soon improves. Young chick gapes in response to parent's touch at base of bill but does not respond to visual stimulus of object brought towards bill. Later, chick gives shrill rattling call and lunges at adult's bill; achieves adult-like squawk at 2–3 weeks (Schreiber and Schreiber 1993). At 3–4 weeks can accept full load from one adult (60–140 g). At 1 week reacts aggressively to intrusion.

FLEDGING: Depending on nature of nest-site, may move out at 5–8 days before fledging and wing-exercise. Or may fledge decisively without exercise. Initial flight to sea unsteady. Fledges between dawn and dusk. Not accompanied by adult and does not return to nest-site. Hand-reared chicks refused food 2–4 days before fledging and 'natural' young lose weight (Schreiber and Schreiber 1993).

Fledging period Kure 85.4 days (78–105) $n = 38$. Johnston 83.7 (78–92) $n = 65$. Midway (1988) 91.3 (77–103) $n = 40$, (1989) 93.8 (83–123) $n = 21$. Aldabra *c.* 90 days. Christmas Island (PO) *c.* 86 days. Christmas Island (IO) *c.* 90 days. Recorded as first flying at 75–84 days and leaving colony at 105 days, which seems highly atypical behaviour for a tropicbird; most leave abruptly on first flight.

POST-FLEDGING: (GFA)

BREEDING SUCCESS: Hatched from laid: Kure 66% (1st layings 1964), 65% (1965). Johnston 90% (1984–92). Midway 60% (1988), 60.4% (1989). Fledged from hatched: Kure 39% (1964), 31% (1965) (but see causes of failure below). Johnston

96% (1967–69), 95% (1984–92). Midway 64% (1988), 68% (1989). Fledged from laid: Kure 64.3% ($n = 700$, 1964), 35% ($n = 1,000$, 1965), 28% ($n = 1,150$, 1966), 32% ($n = 940$, 1968), assuming in all 4 years that 'nests' means nests with eggs. Johnston 80–90% (1984–92)—unparalleled for tropical pelagic seabird. Christmas Island (PO) *c.* 76%. Aldabra (max) 45% ($n = 84$).

Main cause of nesting failure, Kure, Polynesian rat—39 out of 65 eggs, 95% of nestling loss ($n = 72$) (1964, 1965; Fleet 1972). On Midway 68% chick loss due to starvation or (possibly) heat stress, 27% to rats (Tyler 1991, 1996). Some chicks lost to crabs and cats. Some parents fail to change from incubating to chick-care.

FIDELITY TO COLONY, SITE, AND MATE: Most breeders return to or remain in natal colony (recoveries from 15,000+ birds ringed Johnston Atoll show almost no interchange between islands, Schreiber and Schreiber 1993) but significant exceptions. Two birds ringed as breeders on Midway later (3 and 4 years) found breeding on Kure. Recapture rates, or birds known to be alive in year after ringed, very low. Of birds ringed as non-breeders ($n = 1,533$ on Kure 1959–69) percentage known to be alive year following ranged from 4.5–28% (Woodward 1972). Thus, most likely, many or most birds moved on or observations insufficient to record true number remaining, or mortality very high. Of 465 birds ringed as breeding adults percentages known to be alive following year ranged from 6.1–46.2%. Same options apply. On Johnston and Christmas Island (PO) pairs usually remained mated for life (Schreiber and Schreiber 1993) though unsuccessful first-time breeders likely to change mates next year. If movement occurs, fidelity to mate likely to be impracticable. Conversely, where site retained, mate also. Bereaved adult will acquire new mate that year or next, at or near old site. On Kure 83% successful pairs maintained bond 2nd year; only 49% unsuccessful pairs did so (Fleet 1974). Generally return to same nest-site. Where extended breeding season, same nest-site may be used twice in year by different pairs. If pair A return and find site occupied by chick of pair B will evict chick, though this may still be fed by parents or site re-claimed.

AGE OF FIRST BREEDING: Bird ringed as nestling, Oct 1963 on Kure, recovered breeding, Sept 1966, likely to have returned to colony as pre-breeder at least one year previously, that is before fully 2 years old. An even younger breeder (*c.* 9 months) claimed from Johnston, astonishingly early breeding for tropical, pelagic seabird. But likely to be variable. Number first-time breeders (Johnston) increased up to 4 years, then decreased. Oldest first-time breeder definitely 6 (or more) (Schreiber and Schreiber 1993).

NON-BREEDING YEARS: No information but these may well occur.

LONGEVITY AND MORTALITY: Bird aged 23 years 9 months recorded Howland Island (Klimkiewicz and Fitcher 1989). Of 719 recoveries (no correction for ring loss) 6 were 20+ years, 39 aged 10+, 66 were 8+ (Schreiber and Schreiber 1993). Recaptures on Johnston indicate 45% of population over 5 years, 9.5% 10 or more.

Mortality between fledging and breeding can be surprisingly low, especially for pelagic seabird with no parental support after fledging. Schreiber and Schreiber (1993) report 47% of fledged chicks (1983–84 Johnston) returned to breed. Av annual adult mortality not known; circumstantial evidence suggests *c.* 10% or less.

White-tailed Tropicbird *Phaethon lepturus*

PLATE 12

Phaeton (sic) *lepturus* Daudin, 1802, Mauritius.
Other common names: yellow-billed tropicbird, golden or white-tailed bos'n bird, longtail, marlin-spike.
French: phaeton à bec jaune. German: wei bch-wanz-tropikvogel. Spanish: rabijunco menor.

Sub-species

Five often recognized but only one *P. l. fulvus* readily distinguishable and all may be mere colour morphs. *P. l. catesbyi* tropical NW Atlantic and Caribbean. *P. l. lepturus* Indian Ocean. *P. l. fulvus* W and E Indian Ocean and especially Christmas Island where comprises *c.* 92% of population (Stokes 1988). This golden form occurs also on Europa Island (S Mozambique Channel)—only island in W Indian Ocean on which it occurs (Le Corre and Jouventin 1997b, 1999). These authors found that birds from Europa were significantly smaller than *P. l. lepturus* from elsewhere in Indian Ocean and suggest that Europa birds do not belong to either sub-species of Indian Ocean. They divide 5 sub-species of *P. lepturus* into 'large' (*P. l. lepturus*, *fulvus* and *catesbyi*) and 'small' (*P. l. ascensionis* and *dorotheae*). Unexpectedly, Europa birds resemble in size the small sub-group, though neither of the small races occur in Indian Ocean. Thus Europa population seems isolated. *P. l. dorotheae* occurs tropical

Pacific especially in W. *P. l. ascensionis* probably invalid.

Description

ADULT M PRE-BREEDING: Mainly white, sometimes (as Ascension) some males show pink or orange flush; *P. l. fulvus* deep golden. Black band through and behind eye. Black bar top side of wing runs diagonally from carpals to tertials. White below. Elongated central feathers of pointed white tail (some birds Caribbean, Atlantic have reddish tail streamers). Bill usually yellow but may be orange, reddish in Caribbean and Atlantic or nondescript. Eye dark brown. Legs pale greenish, webs blackish or yellowish. N Atlantic birds have most black on primaries. W Indian Ocean birds larger than type, W Pacific birds smaller. Stonehouse (1962) noted striking variation in colour of plumage, feet, bill of Ascension birds.

ADULT F: Similar to M, though whiter on Ascension.

POST-NUPTIAL: Little change.

JUVENILE AND IMMATURE: Heavily barred black-on-white on nape, hind-neck, mantle, rump; barred inner upperwing forms triangular patch on leading

edge. Tail white with black terminal spots and (perhaps) slightly projecting central feathers. 12 tail feathers differentiates from red-billed (14). Bill dull yellow with black tip. Few details on intermediate plumages; separable from adults for two or three years.

Field characters

Smallest tropicbird; slender; long, angular wings with diagnostic black bar; yellow bill. From below translucent wings may reveal shadows of black on upperwing. Juv lacks distinct collar of red-billed and has heavier barring on upperparts. Juv red-tailed less black on primaries. Both species larger with heavier flight.

Measurements (see Appendix)

Moult

Moults body feathers completely after successful breeding. May moult some flight feathers whilst

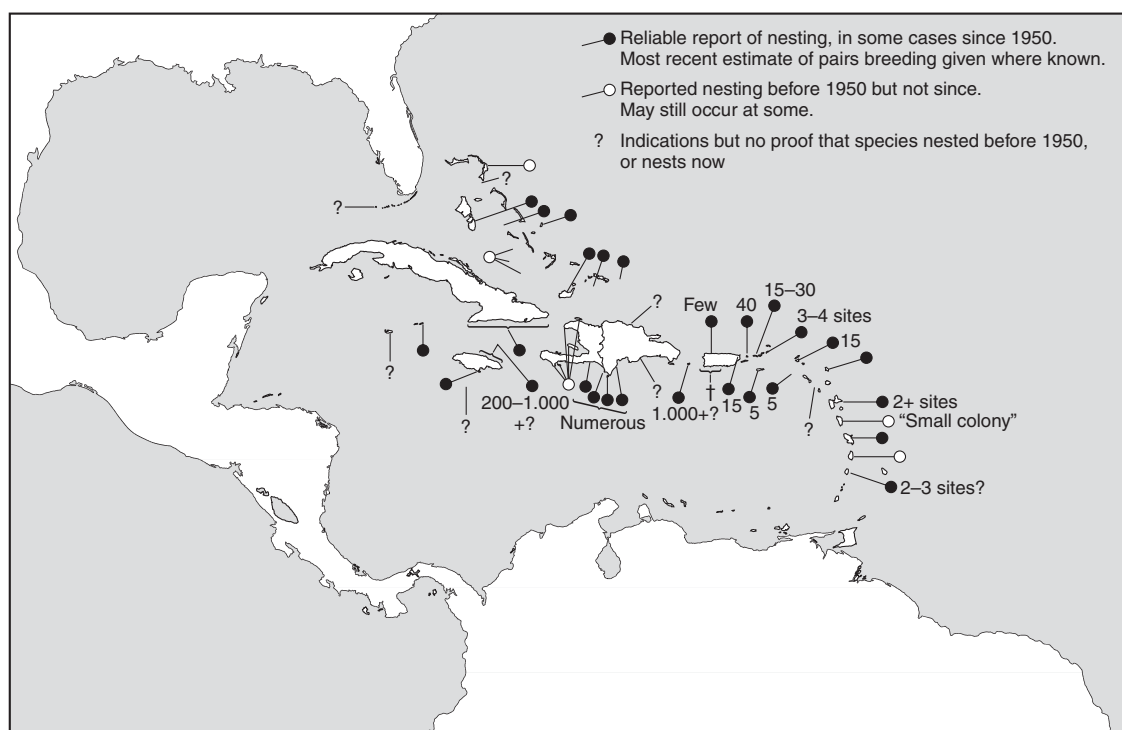
breeding and many birds, at their sites after long absence at sea, were growing one or more outer primaries (6–10). In a few such birds even body moult was incomplete (Stonehouse 1962). Thus, at least on Ascension, energy demands of moult evidently compatible with those of breeding despite evidence that breeding cycle particularly demanding. On Aldabra (Diamond 1975b) 'very few' birds in active wing moult whilst incubating or rearing chick. Tail feathers moult independently of wings and body.

Voice

Adult guttural 'clicks' and 'chucks'; short 'chuckles' when displaying.

Range and status (Figure 5.41; 6.165)

Probably commonest tropicbird. Pantropical throughout central and W Pacific, tropical Indian Ocean mostly S of equator to 25°, tropical Atlantic



6.165 Breeding distribution of the white-tailed tropicbird in the Caribbean (10,000+ pairs). (From Halewyn and Norton 1984.)

to 32°N in Bermudas. Recently recorded Cape Verdes (Hazevoet 1999). Total S Atlantic population probably fewer than 3,000 pairs, but 1,000+ pairs on Ascension. Breeds Fernando Noronha and *c.* 86 pairs St Helena. Present on some islands Gulf of Guinea along with red-billed. Fernando Po needs checking as possible breeding place (above from Croxall *et al.* 1984). Guesstimated 10,000 pairs in Caribbean where population thought to be stable. Absent from W Caribbean and rare in Gulf of Mexico. In Caribbean range distinct from red-billed in particular in Greater Antilles from E Cuba to Mona Island and including Jamaica. Colonies on Bermuda particularly dense. Recently breeding Isla del Coco (Costa Rica) (Dudzik 1995). Common breeder S coast Hispaniola (van Halewyn and Norton 1984). Few colonies in Bahamas exceed 50 pairs but altogether number in low thousands (Sprunt 1984). Recent estimate for Christmas Island (IO) of up to 12,000 pairs seems too optimistic (see Stokes 1988). Feare (1984) summarizes breeding localities in tropical Indian Ocean: Aldabra (1,000–10,000 pairs), Comores (breeds on 4 islands), Seychelles in general (10,000+ pairs), Mascarenes (100–1,000 pairs), Maldives, Chagos, Cocos Keeling (fewer than 100 pairs). Le Corre and Jouventin (1997b) estimated 500–1,000 pairs on Europa (Madagascar). Pacific Islands may hold several thousand pairs. Occurs S of Java in Banda Sea and in Coral Sea. Christmas Island birds go as far as 1,300 km to the SE and to waters off NW Australia (Pocklington 1979; Dunlop *et al.* 1988). Whilst overall numbers have declined this century some colonies have apparently remained stable.

MOVEMENTS: Disperses widely outside breeding season. No evidence strongly directional movements. Most breeders seldom seen after chick fledges. Rare straggler to New Zealand (nearest breeding Niue Island). 10 dead birds found by beach patrol (1943–88), 5 of them immature, after strong northerlies. Regularly seen Fiji–New Zealand to 21°S. Occasional in offshore and pelagic zone off New South Wales.

Foraging and food (GFA)

Usually feeds singly or in twos. Some populations tend to feed closer to breeding island than red-tailed

and may be more prone to join mixed flocks of boobies, terns, and petrels. Radio tracking followed birds out to 176 km from colony (Pennycuik *et al.* 1990); energy consumption was increased by carrying transmitter (doubly labelled water method).

Based on Pennycuik's equations (1975, 1989) and white-tailed tropicbird's mass and wingspan, Schaffner (1990b) proposes air-speed of 46 kmph; this would maximize distance flown per unit of fat consumed. He calculated energy contained in av feed-mass is about twice cost of 50 km trip back to nesting colony, in still air at optimal speed. Much longer trips transporting this amount become energetically uneconomical and impractical in terms of delayed digestion, which shows that long absences are spent largely in self feeding. However, total travel time and energy costs per trip for given flight distance and wind condition increase only marginally with substantially increased mass of deliverable food. White-tailed tropicbirds are capable of transporting feeds more than twice size of overall mean feed-mass (0.052 kg or 14% of unladen adult body-mass).

Deep plunges from up to 20 m or pursuit plunges. Flying fish taken in flight. Fish form *c.* 16% of diet by weight depending on region and cephalopods (on Aldabra all Ommastrephids) 11–85%; proportion (by weight) increasing in wet season up to 90.7% (Diamond 1975b). *Exocoetus volitans* (up to 25 cm) and *Cypselurus bahiensis* important. Other recorded prey, with size ranges, from Ascension, Bermuda, Christmas Island (IO), Aldabra and other Seychelle Islands in Marchant and Higgins (1990).

Habitat and breeding biology

(See Fig at end of ch. 5; Ascension—Stonehouse 1962; Aldabra—Diamond 1975b; Cousin (Seychelles)—Phillips (1987); Cayo Luis Pena (Puerto Rico)—Schaffner 1990b, 1991; Christmas Island (IO)—Stokes 1988; personal observation.

HABITAT: Tropical and sub-tropical oceans, breeding on islands and atolls, variable height. Will use bare ground, among rocks or vegetation, in cliff-holes, on cliff-ledges or in tree crotches or cavities in rainforest of Christmas Island. In Hawaii nests miles inland in eroded Waimea Canyon and in

steaming volcanic crater of Halemauan. Prefers to fly directly to site; walks with difficulty. Where breeds with another tropicbird species may compete strenuously (Ascension) or utilize specialized niche (Christmas Island, IO). Marine preferences probably similar to other tropicbirds (GFA).

COLONIES: Small or moderate, rarely more than 1,000 or so pairs, within which comparatively well spaced. Often, present size of colony artefactual due to persecution. Detailed study, Puerto Rico, (Schaffner 1991) showed nearest-neighbour distances (nest-sites) 2–4 m along 170 m of coast at one colony, 6–10 m along 420 m at another. Nests av within 6 m of waterline, 2 m above high tide.

FREQUENCY, TIMING, AND DURATION OF BREEDING: Suggestion of cycles of 7–8 months on Aldabra. On Christmas Island (IO) shows 10-month breeding periodicity (Reville and Stokes 1994). In Caribbean nesting activity continued over 6 months peaking mid-May though apparently unsynchronized. Pre-laying preliminaries (site-establishment and pair-formation) take 2–8 weeks. Partners absent between mating and laying for some 21 days (18–30) $n=30$. Successful cycle-length av 9.5 months on Ascension; intervals between successive successful layings 35–47 weeks, two-thirds 37–9 weeks. May begin new cycle after loss of small chick (13% on Cousin) without normal interval and without intervening moult. Minimum interval between loss and replacement same as between mating and laying (*c.* 17 days). For pairs which did not re-nest almost immediately, mean interval between failure (egg or chick) and next breeding did not differ significantly from that between producing successful fledgling and beginning next attempt, though more variable. Disperses after breeding for moult (and recuperation?); 16–21 weeks. On Cousin, adults lost weight during at least first 20 days of chick's life after which tended to regain weight. Lifetime breeding frequency not known. Breeds throughout year in Seychelles with no consistent periodicity. On Christmas Island (IO) nests in all months apparently without marked preference (Stokes 1988) (Powell, personal communication, recovered adults

grounded in rainforest, presumably breeding, every month except May, September and October and juveniles only April to August). On Ascension laying peaks periodic but non-seasonal.

TERRITORIAL, PAIR-FORMATION, AND MAINTENANCE: Approx 2–5 weeks, mostly 2–3, between return to nest-site and egg-laying. Overt fighting for territory may be severe and injurious, often occasioned when previous occupier returns after its dispersal at sea to find site usurped; may kill young of usurping pair. Thus shows strong attachment to site but may lose it in competition with conspecific or red-billed. In turn may evict *e.g.* Bermudan petrel from hole. Fights with interlocked bills and spread wings. At Cousin (Seychelles) most sites used by only one pair; little evidence of competition. On Aldabra (Diamond 1975b) little overlap between this species and red-tailed which tended to choose more open sites. Sites may be visited by pairs which do not breed that year but may subsequently be used (Schaffner 1991).

Aerial courtship reported to continue 2–5 weeks before egg laying. Usually involves fewer than 10 birds in zig-zag flight with long downward glides; on Christmas Island (IO) above and within tree cover. No detailed analysis available (GFA). Aerial display between mates not confined to courtship period; occurs in about half of cases where parents return to nest in same time period. Schaffner suggests necessary for mates to make periodic contact if continued feeding of chicks to be assured and in fact breeding adults with chicks, perhaps particularly males, may make non-feeding visits possibly for this purpose (though loss of food to frigatebirds may precede a non-feeding visit).

COPULATION: (GFA)

NEST: (GFA) Mere scrape; adjacent to crevice opening or up to several m within it. Measurements for nest cavities (Burgher and Gochfield 1991) on Round Island, Mauritius, showed av cavity height 59.5 cm, width 48.5, depth 38.5, 80% shade $n=6$. On Aldabra occupied smaller cavities on small islets than red-tailed. Used 'solution' holes

or laid on surface, between tussocks of *Sclerodactyla macrostachyum*.

EGG/CLUTCH: Always one; ovoid, dull, pale fawn or rich purple-brown ground colour with red-purple spots or blotches: 54 (46.4–62.2) × 38 (33.9–41.3); 53 × 38; 48–53.5 × 37–40 n = 6; 50 × 36; 54 × 40; 54 (46.4–62.2) × 38 (33.9–41.3) n = 811. Weight 43.4 g n = 10 (Aldabra); 40 g (Bermuda); 41 g (Ascension); up to 13% female weight (only 10% in Bermuda). Replacement n = 45 4–5% by vol smaller than originals by same females.

REPLACEMENT LAYING: On Cousin Island 21% of birds losing eggs and 13% of those losing chicks re-laid after about same interval as occurred between mating and laying of first egg. Mean age of lost eggs replaced 'immediately' was 15.5 (1–40 days) and of eggs not replaced 30.2 (4–40). On Ascension eggs were replaced 23–30 days after loss. On Aldabra 47 ± 5 n = 3, 41 or less, 51 or less.

INCUBATION: (GFA) 40–3 days, mainly 41–2. In Caribbean 40.7 ± 1.2; 41.2 ± 0.86 and 41.2 ± 0.86. On Cousin female's first shift 4.3 days (1–13), male 8.5 (6–11). Subsequently female 6.6 (3–10), male 7.4 (4–11). On Ascension shifts 3–4 days.

CARE OF YOUNG: Closely broods hatchling, though some unattended 1st day. May feed it within first 12–16 hours. Uniquely for a pelecaniform, places food in chick's gape. Great variability in pattern of chick feeding. Some males feed it daily, some females miss several consecutive days. Food transfer can be rapid (<30 sec for major bolus); adults usually out in less than 3 min. Spilt food not retrieved. By day 4–5 parental visits restricted to 1–2 per day. Some very young chicks may thus be exposed to hot sun; protected by down but some die (Phillips 1987).

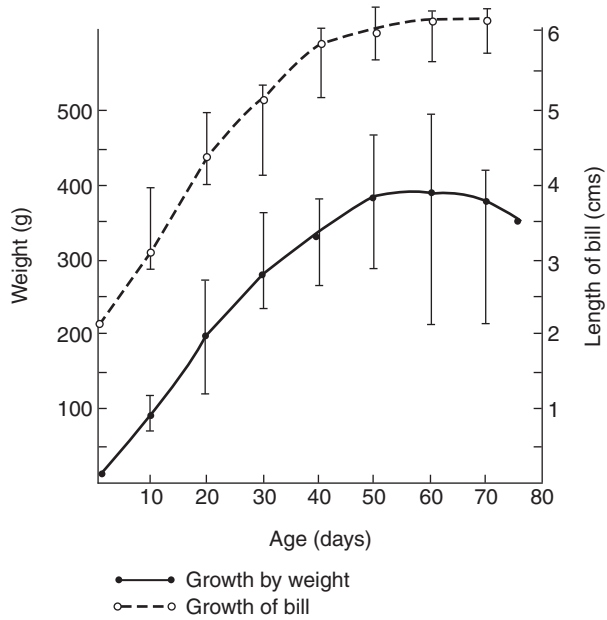
BEHAVIOUR OF YOUNG: Few details. Seeks shade if exposed. Large young defend site against intruders.

FLEDGING: (GFA) Flies directly from nest-area out to sea, alone. Not known to return to nest-site. Cousin 76.5 (67–89) days; Aldabra c. 80; Ascension and Christmas Island (IO) c. 75; Puerto Rico 73 ± 5.25, 71 ± 2.65, 71 ± 1.57 (1984–86).

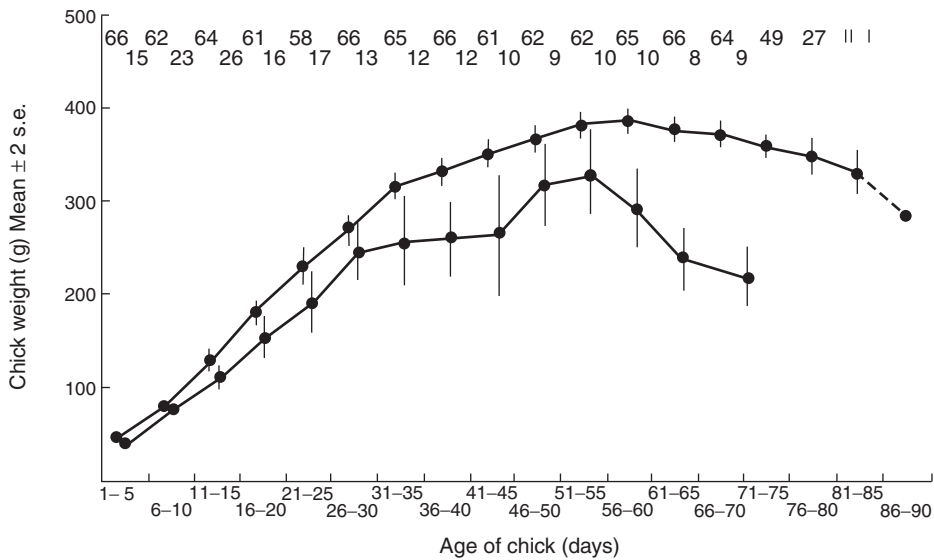
CHICK: c. 30 g with long, silky white or grey down; appears blind. Attended 70–90%+ of time week 1, 24% by weeks 3–4 decreasing to little or none after 4–5 weeks but details vary with area. May receive first feed with 12 hrs and fed daily at first then less frequently but this varies. Some adults seen to feed chick twice within single daylight period, with intervening foraging trip. On Ascension, weight of individual feeds (chick regurgitations): 30–50 g (chick 11–20 days), 40–70 (21–30 days). Large chicks can accommodate flying fish up to 30 cm long. Stonehouse (1962) provides details (Atlantic) of growth by weight and bill (Figure 6.166) whilst Phillips (1987) contrasts growth successful v unsuccessful chicks (Indian Ocean) (Figure 6.167). Chicks (Atlantic) reach adult mass c. 35 days and lay down large but highly variable amounts of fat until c. 55–60 days after which most lose weight until they fledge which often (normally?) occurs after several days unfed though observations disagree. Max mean weight c. 400 g (121–126% adult weight); some chicks heaviest as many as 45 days before fledging whilst others only just prior. Fledging weight c. 330 g (much as adult). Max weight and fledging weight highly correlated. Comparable parameters for Indian Ocean in Figure 6.167. Schaffner (1990b) gives details of correlation between pattern of food provisioning and development of chick. Also suggests general mechanism for fat deposition in tropical pelagic seabirds (correlate of intermittent feeding). Suggests meal-size in tropicbirds limited by chicks' ingestive capacity; not by limits on adults' ability to catch or transport more.

POST-FLEDGING: (GFA)

BREEDING SUCCESS: Hatched from laid: Cousin 61.2%; Ascension 48.1% (n = 821); Puerto Rico 55.9%, 50.7%, 42%, 53.7% (1983–86). Fledged from hatched: Ascension 82.2% (n = 395); Puerto Rico 79% (n = 19), 81.8% (n = 33), 93.3% (n = 30), 80.6% (n = 36). Fledged from laid (variable but usually fairly low): Cousin 36%; Aldabra 47.5% (2 seasons); Ascension 30.3%; Puerto Rico 44.1%, 41.5%, 39.1%, 43.3% (1983–86). Most figures maxima because exclude nests that started and failed between observer visits. Failure mainly due



6.166 Growth of the white-tailed tropicbird (Atlantic). (After Stonehouse 1962.)



6.167 Weights of white-tailed tropicbird chicks which were successful (upper curve), compared with failures (Indian Ocean). Figures above mean points are sample sizes. (From Phillips 1987.)

to loss of eggs (conspecific interference, desertion usually at end of first full incubation shift, predation by rats and crabs) and chicks under 10 days (hawks, frigates, crabs, rats, cats). Large chicks deserted if 10–18 or more days elapse between last feeding by one parent and last (of 3 or 4 given in intervening period) by its mate (Schaffner 1991). On Aldabra exposure to sun probably killed some embryos, desertion by heat-stressed adults many more. Many losses due to interspecific site competition on Ascension, intraspecific on Aldabra and Puerto Rico. Of chick deaths, 71% (Cousin), 55% (Ascension) occurred in first fortnight, some at critical hatching time.

FIDELITY TO COLONY, SITE, AND MATE: Probably depends on locality. On Cousin most individuals nested on same site, with same partner, in successive breeding attempts (Phillips 1987); only 7.5% of nest-sites used by more than one pair, so competition not

extreme, *contra* some localities. On Ascension natal philopatry would be expected to be strong. Here, too, strong attachment to nest-site though some move small distances. On Aldabra, by contrast, many sites used once then left unused—sometimes for years. Where site fidelity high, mate fidelity can be similarly so.

AGE OF FIRST BREEDING: At least 2 years. Probably more usually 3–4.

NON-BREEDING YEARS: Probably some non-breeders at colony. Schaffner (1991) indicates substantial turnover, suggesting ‘rest’ years; in 1984–88 out of 104 active sites and 110 onesting pairs, only *c.* 60% nested in any one year.

LONGEVITY AND MORTALITY: Av life expectancy probably at least 10–15 years. Pre-breeding mortality probably high; adult mortality low.

Appendix: Measurements

Pelicans

Great white pelican

Wing: M (skins) 684 (665–672) n = 24; 734 (680–770) N Caspian. F 620 (586–650) n = 17; 677 (600–780) N Caspian. Tail: M 176 (155–188) n = 5; 194 (170–230) N Caspian. F 162 (138–178) n = 7; 181 (160–205) N Caspian. Bill: M 409 (347–471) n = 9; 432 (350–432) N Caspian. F 328 (289–400) n = 14; 341 (300–460) N Caspian. Tarsus: M 145; 146; 149; 146 (120–185) N Caspian. F 132 (125–145) n = 6; 129 (100–165) N Caspian.

Weight: M up to 11,000 g; 9000–15,000; 10,200 (5500–13,000). F up to 10,000; 5400–9000; 5100–7900. Obviously hugely variable, much depending on how recently fed.

Pink-backed pelican

Wing: M 605 (595–615) n = 5. F 560 (545–580) n = 6. Tail: M 172 (160–185) n = 5. F 166 (140–180) n = 7. Bill: M 357 (335–375) n = 19. F 305 (230–335) n = 68. Tarsus: M 96 (90–100). F 87 (75–100).

Weight: M 6000 g (4500–7000) n = 19. F 4900 (3900–6200) n = 64. Unsexed adults 5200 n = 83.

Spot-billed pelican

Wing: M 530–607. F 525–550; 560. Tail: M 168–198. F 180. Bill: M 324–355. F 285–308. Weight: M 5100 g; 5700 (captive). F 4650.

Dalmatian pelican

Wing: M 717 (710–730) n = 4; 745 n = 15. F 710 n = 1; 725 n = 15; 670–780 n = ?, 690–800 n = ?. Tail: M 240 (230–250) n = 4. F 230 n = 1. Bill: M 436 (420–450) n = 4; 420 n = 15; 390–450 n = ?. F 440 n = 1; 390 n = 15; 350–430 n = ?. Tarsus: M 131 (130–135) n = 4. F 130 n = 1. Weight: M 9200 (7300–10,800) n = 15; 10,500; 10,500; 11,500; 12,000. F 8400 (7500–10,000) n = 13. Juv 9100 n = 4.

Australian pelican

Wing: M 637.8 (560–690) n = 132; 659.6 (642–682) n = 6 (skins). F 581.2 (541–605) n = 25; 606.6 (580–641) n = 5 (skins). Tail: M 181.8 (154–225) n = 6 (skins). F 165.7 (147–182) n = 4 (skins). Bill: M 453.3 (410–495) n = 260; 459.5 (430–496) n = 6 (skins). F 382.3 (355–408) n = 34; 407.4 (363–456) n = 5

(skins). Tarsus: M 115.4 (100–150) n = 98; 133.8 (126.1–141) n = 7 (skins). F 107.5 (95–125) n = 21; 124.5 (120–127.7) n = 5 (skins). Weight: M c5800 g but up to 7650 g. F no data but probably usually around 4900 g calculated on ratio of M:F measurements.

American white pelican

Wing: M 608.2 (575–630) various localities. F 558.5 (525–603). Tail: M 159.7 (153–167). F 144.8 (135–166). Bill: M 342.3 (320–365). F 287.6 (265–320). Tarsus: M 122.5 (115–130). F 115.7 (108–123). Weight: huge variation between 4500 g and 13500 g. Commonly 6000–8000 g with M much heavier than F.

Brown pelican

Extremes (all races)

Wing:	M 461 (<i>occidentalis</i>)–625 (<i>thagus</i>).	F 448–606.
Tail:	M 114–177.	F 114–174.
Bill:	M 255–425.	F 251–390.
Tarsus:	M 70–89.4.	F 68–83.7.

Races

Occidentalis Wing: M 478 n = 16. F 462 n = 14. Tail: M 126 n = 16. F 124 n = 14.

Bill: M 288 n = 16. F 261 n = 14.

Murphyi Wing: M 513 n = 11. F 485 n = 8. Tail: M 135 n = 11. F 139 n = 8. Bill: M 328 n = 11. F 293 n = 8.

Carolinensis Wing: M 526 n = 28. F 501 n = 23. Tail: M 136 n = 28. F 136 n = 23. Bill: M 319 n = 28. F 294 n = 23.

Californicus Wing: M 551 n = 34. F 519 n = 23. Tail: M 154 n = 34. F 151 n = 23. Bill: M 347 n = 34. F 312 n = 23.

Urinator Wing: M 561 n = 9. F 527 n = 5. Tail: M 140 n = 9. F 137 n = 5. Bill: M 361 n = 9. F 329 n = 5.

Thagus Wing: M 606 n = 6. F 576 n = 14. Tail: M 152 n = 6. F 146 n = 14. Bill: M 397 n = 6. F 354 n = 14. Weights.

Occidentalis: M 2160–3000. F ?

Carolinensis: Ad M 3290 (2380–4040) n = 13. Imm M 2628 (1950–4240) n = 12. Ad F 2824 (1830–3990) n = 13. Imm F 2316 (1400–3800) n = 16.

Californicus: Ad and sub-ad M 5044 (2806–9750) n = 5. F 3769 (2721–4623) n = 5.

Thagus: M 7030 n = 1. F 5055, 5500, 3316.

Sulids

Australasian gannet

Wing: M 463 (443–482) n = 14; 469.6 (440–485) n = 13. F 471.7 (455–480) n = 7. Tail: M 212 (206–218) n = 14; 215.3 (203–228) n = 8. F 213 (200–230) n = 7. Bill: M 89 (85–93) n = 14; 90.9 (87–93) n = 12. F 89.7 (85–95.5) n = 8. Tarsus: M 54 (51–57) n = 14; 55.7 (51–59) n = 13. F 57.5 (54.3–62.6) n = 7. Weight: Unsexed 2350 (2000–2800) n = 44; unsexed 2456 (2280–2800) n = 7; Nov 2456 (2100–2750)

n = 13; Dec 2258 (2000–2600) n = 19; Jan 2230 (2100–2500) n = 5. A hint, here, that weight lost during breeding; also that female marginally larger than male—a booby trait.

African gannet

Wing: M 480 (450–510) n = 20. F 477 (up to 510) n = 16. Tail: M 189 (180–205) n = 16. F 191 (up to 206) n = 30. Bill: M 94 (90–100) n = 10; 92 (88–97) n = 43. F 91 (85–100) n = 10; 91 (up to 97) n = 51. Weight: M 2618 (2296–2920) n = 61; 2665 (2523–3005) n = 55. F 2669 (2381–3118) n = 53; 2608 (2240–3219) n = 61.

Atlantic gannet

Wing: M 513 (500–535) n = 9 Bass Rock, 501 (487–511.5) n = ? Bonaventure. F 510.2 (484–522.4) n = 14 Bass Rock, 496 (485–503) n = ? Bonaventure. Tail: M and F 214.5 (189.5–225.5). Bill: M 100.1 (93.5–110) n = 66 Bass Rock, 98.2 (92.5–104) n = 22 Ailsa Craig, 101.7 (93.5–107) n = 37 Bonaventure. F 99.2 (92.5–104) n = 66 Bass Rock, 97.7 (92.5–100.4) n = 23 Ailsa Craig, 101.7 n = 24 Bonaventure. Tarsus: M 50.2 (48.5–51) n = 3 Bass Rock, 62.5 (59–65) Bonaventure. F 50.8 (47–59) n = 12 Bass Rock. Weight: M 2932 (2470–3470) n = 27 Bass Rock, 3120 (2400–3600) n = 17 Ailsa Craig, 3153 n = 38 Bonaventure. F 3067 (2570–3610) n = 27 Bass Rock, 2941 (2300–3600) n = 18 Ailsa Craig, 3284 n = 24 Bonaventure.

Abbott's booby

Wing: M 445.5 (440–464) n = 5 (live birds, mine); 438.4 (432–447) n = 5 (various skins and workers). F 454.3 (434–493) n = 17 (live birds); 450.9 (435–462) n = 8 (various skins). Tail: M 208 (195–220) n = 5 (live); 217.2 (200–247) n = 6 (skins). F 202.7 (191–215) n = 14 (live); 225.0 (203–265) n = 11 (skins). Bill: M 106.3 (101.5–108.5) n = 8 (live); 109.6 (108–112) (skins). F 111.2 (104–120) n = 18 (live); 112.4 (110–116) n = 8 (skins). Tarsus: M 41.6 (39–45) n = 3 (live); 48.7 (42–51) n = 3 (skins). F 46.3 (40–50.2) n = 13 (live); 45.6 (43–48) n = 5 (skins). Weight: M 1472.6 (1336–1620) n = 5 (live); 1410.4 (1300–1620) n = 8 (grounded birds, weight loss unknown). F 1491.5 (1293–1724) n = 15 (live); 1467.6 (1248–1724) n = 17 (grounded birds).

Red-footed booby

Wing: M 379 (344–395) n = 44. F 386 (370–419) n = 23. Tail: M 212 (183–243) n = 34. F 206 (177–245) n = 18. Bill: M 82.5 (72–92) n = 63. F 87.3 (80–95) n = 45. Tarsus: M 35.7 (32–41) n = 30. F 40.2 (34–47) n = 16. Weight: M 881 (803–1160) n = 29. F 944 (766–1210). N.B. much regional variation not differentiated in above. Ballance (1995) provides figures for wing-span (1.51 m); wing-area (0.2 sq m) aspect ratio (11.4) and wing-loading (51.5) derived from measurements and body mass.

Masked booby

Wing: M 424 (406–433) n = 9 *S. d. dactylatra*; 421 (407–430) n = 6 *S. d. melanops*; 428 (424–434) n = 4 *S. d. bedouti*; 440 (427–462) n = 27 *S. d. personata*; 429 (413–443) n = 5 *S. d. granti* Galapagos; 451 (445–457) n = 6 *S. d. granti* Galapagos; 444 n = 1 *S. d. fullageri*. F 429 (417–440) n = 7 *S. d. dactylatra*; 456 (435–476) n = 27 *S. d. personata*; 450 (427–468) n = 6 *S. d. granti* Galapagos; 484 (457–495) n = 5 *S. d. granti* Galapagos; 471

(453–486) n = 4 *S. d. granti* Chile. Tail: M 166 (153–173) n = 9 *S. d. dactylatra*; 176 (169–180) n = 6 *S. d. melanops*; 189 (184–193) n = 4 *S. d. bedouti*; 188 (170–215) n = 27 *S. d. personata*; 178 (172–181) n = 5 *S. d. granti* Galapagos; 198 (192–205) n = 5 *S. d. granti* Galapagos; 198.7 n = 1 *S. d. fullageri*. F: 164.6 (151–180) n = 7 *S. d. dactylatra*; 192 (173–205) n = 27 *S. d. personata*; 183 (176–189) n = 6 *S. d. granti* Galapagos; 201 (185–212) n = 5 *S. d. granti* Galapagos; 192 (188–196) n = 4 *S. d. granti* Chile. Bill M: 95.6 (92.6–97.2) n = 9 *S. d. dactylatra*; 100.7 (97–104) n = 6 *S. d. melanops*; 100.9 (97.5–104) n = 4 *S. d. bedouti*; 102.7 (97–107) n = 27 *S. d. personata*; 102.7 (102–104.4) n = 5 *S. d. granti* Galapagos; 106.8 (88–113) n = 47 *S. d. granti* Galapagos; 110.3 n = 1 *S. d. fullageri*. F 95.7 (91.6–99) n = 7 *S. d. dactylatra*; 105 (98–109) n = 27 *S. d. personata*; 106.5 (102–114.5) n = 6 *S. d. granti* Galapagos; 109.3 (105–115) n = 36 *S. d. granti* Galapagos; 104.1 (100.5–108.4) n = 4 *S. d. granti* Chile. Tarsus: M 54 (53–56) n = 9 *S. d. dactylatra*; 56 (51–58) n = 6 *S. d. melanops*; 51 (48–53) n = 4 *S. d. bedouti*; 63.6 (60–67) n = 27 *S. d. personata*; 55 (52–58) n = 5 *S. d. granti* Galapagos. 58.6 (n = 1) *S. d. fullageri*. F 53.4 (52–54.6) n = 7 *S. d. dactylatra*; 65.2 (60–70) n = 27 *S. d. personata*; 57 (54–59) n = 6 *S. d. granti* Galapagos; 58.7 (57–61) n = 4 *S. d. granti* Chile. Weights: M 1565 (1480–1660) n = 6 *S. d. melanops*; 1880 (1503–2211) n = 27 *S. d. personata*; 1627 (1220–1970) n = 48 *S. d. granti* Galapagos. F 2095 (1616–2353) n = 27 *S. d. personata*; 1881 (1470–2350) n = 37 *S. d. granti* Galapagos.

Blue-footed booby

Wing: M 431.8 (406.4–438.2) n = 9 Galapagos; 406.7 (394–421) n = 10 Panama to Peru; 420.1 (410–426) n = 3 Mexico. F 457.2 (431.8–469.9) n = 8 Galapagos; 423.3 (403–438) n = 7 Panama to Peru; 428.4 (404–449) n = 8 Mexico. Tail: M 236 (223–251) n = 18 Galapagos; 190.6 (165–226) n = 10 Panama to Peru; 211.1 (198–221) n = 3 Mexico. F 237 (223–250) n = 19 Galapagos; 184.1 (163–220) n = 7 Panama to Peru; 207.1 (201–214) n = 3 Mexico. Bill: M 106 (100–111.5) n = 21 Galapagos; 100.4 (95–107) n = 10 Panama to Peru; 108.7 (106–111) n = 3 Mexico. F 114 (111–120) n = 27 Galapagos; 106.1 (95–110) n = 7 Panama to Peru; 109.4 (106–114) n = 8 Mexico. Tarsus: M 51.4 (49–56) n = 10 Panama to Peru. F 54.1 (53–55) n = 7 Panama to Peru. Weight: M 1283 (1100–1,580) n = 23 Galapagos; 1332 n = 2 Panama to Peru. F 1801 (1450–2230) n = 28 Galapagos; 1680 n = 2 Panama to Peru.

Peruvian booby

Wing: M 379.5 (361–394) n = 14. F 395.4 (378–415) n = 9. Tail: M 163.5 (146–181) n = 14. F 172.5 (161.5–190) n = 9. Bill: M 92.6 (88–99.6) n = 14. F 98.2 (96–101) n = 9. Tarsus: M 48 (45–50) n = 14, 40 n = 2. F 50.4 (48–53) n = 9. Weight: M 1300 (1250–1350) n = 2. F 1520 (1500–1540) n = 2.

Brown booby

S. l. leucogaster Wing: M 381 (372–391) n = 13 (various localities); 395 (383–415) n = 9 (Brazil); 392.2 (378–411) n = 10 (Cape Verdes); 370–410 n = 14 (Ascension). F 400 (384–415) n = 10 (various localities); 401.8 (389–413) n = 10 (Brazil); 404.3 (395–412) n = 10 (Cape Verdes); 390–420 n = 26 (Ascension). Tail: M 186 (169–198) n = 13 (various localities); 193.7 (181–203) n = 9 (Brazil); 190 (173–208) n = 10 (Cape Verdes). F 180.5 (162–198) n = 10 (various localities); 191.4 (183–200) n = 10 (Brazil); 191.5 (177–200) n = 10 (Cape Verdes). Bill: M 92.7 (87.8–101) n = 13 (various localities); 93.5 (90–99) n = 9 (Brazil); 94.7 (90–100) n = 10 (Cape Verdes); 87–91 n = 14 (Ascension). F 93.3 (91.8–102) n = 10 (various localities); 94.2 (90–100) n = 10 (Brazil); 100.1 (97–102) n = 10 (Cape Verdes); 91–99 n = 26 (Ascension). Tarsus: M 44.3 (42–48.4) n = 13 (various localities); 45.6 (44–49) n = 9 (Brazil); 47.9 (45–51) n = 10 (Cape Verdes). F 46.8 (45–48) n = 10 (various localities); 46.9 (45–49) n = 10 (Brazil); 48.8 (47–51) n = 10 (Cape Verdes).

S. l. brewsteri (Clipperton and Tres Marias) Wing: M 380 (365–398) n = ?. F 416 (385–440) n = ?. Tail: M 186 (172–196) n = ?. F 191.2 (182–206) n = ?. Bill: M 92.4 (84–97.4) n = ?. F 99.3 (92.6–110.2) n = ?.

S. l. etesiaca (various localities) Wing: M 376 (365–382) n = 6. F 395.5 (360–412) n = 11. Tail: M 179.1 (168–187) n = 5. F 190.8 (174–198). Bill: M 92.5 (87–95) n = 6. F 98.4 (93–102) n = 11. Tarsus: M 44.9 (43–50) n = 6. F (44–50) n = 11.

S. l. plotus (Cocos Keeling and Christmas Island) Wing: M 394.9 (379–428) n = 25. F 416 (385–440) n = 21. Tail: M 208.2 (196–236) n = 23. F 206.2 (190–227). Tarsus: M 42.0 (40.0–44.0) n = 13. F 44.6 (44.0–47.0) n = 13.

Weight: *S. l. leucogaster* (Ascension) M 850–1200 n = 14. F 1100–1550 n = 26.

S. l. plotus (Christmas Island) M 962 (850–1190) n = 20. F 1260 (970–1480) n = 29.

Cormorants and shags

Double-crested cormorant

Race unspecified. Wing: M 311 (302–333); 272–349; 316.4 ± 0.4 n = 759. F 303 (285–321); 260–340; 300.3 ± 0.36 n = 372. Tail: M 123–165. F 120–156. Bill: M 57 (52–60); 47–63; 58.4 ± 0.12 n = 760. F 53 (51–55); 42–61; 54.3 ± 0.15 n = 375. Tarsus: M 61 (59–65); 49–72. F 60; 50–71. Weight: M 2089.3 ± 5.32 n = 763. F 1831 ± 7.17 n = 375. *P. a. albociliatus* Wing: M 311 (255–332) n = 19. F 297 n = 12. Bill: M 57.4. F: 55.2. Tarsus: M 64 (61–71). F 60. Weight: M 2453 (2200–2750) n = 16. F 2056 (1750–2400). *P. a. auritus* Wing: M 311 (302–333) n = 11. F 303 n = 8. Bill: M 57. F 53. Tarsus: M 61 (59–65). F 60. Weight: M 2415 (1986–2807) n = 12; 2233 (2072–2566) n = 10. F 2287 (1758–2948) n = 3; 1861 (1732–2026) n = 12. *P. a. cinctatus* Wing: M 331 (312–349) n = 9. F 334 n = 4. Bill: M 59. F 58. Tarsus: M 68 (64–72). F 66. *P. a. floridanus* Wing: M 303.1 (282–316) n = 32; 299 (282–310) n = 5. F 288.9 (275–305) n = 17. Bill: M 56.5 (47–61) n = 32. F 54.6 (51–60) n = 19. Tarsus: M 57 (56–60) n = 5. Tail: M 144.3 (130–157) n = 30. F 135.5 (125–152) n = 15. Weight: M 1849 (1440–2100) n = 9; 1758 (1327–2079) n = 6. F 1650 (1150–2080) n = 9; 1535 (1391–1665). *P. a. heuretus* Wing: M 270.6 (260–280) n = 8. F 263.1 (259–276) n = 8. Tail: M 143.8 (123–132) n = 4. F 121.9 (117–132) n = 7. Tarsus: M 54 (49–57). The most important variables for identifying sex (96.5% accuracy) are, in order, wing-length, culmen depth and culmen length.

Neotropic cormorant

P. b. brasiliensis Wing: M 283.3 (271–305) n = 28. F 270 (250–282) n = 18. Tail: M 166.6 (144–181) n = 28. F 154 (139–175) n = 18. Bill: M 57 (54–61) n = 28. F 54 (49–58) n = 18. Weight: (unsexed) 1260 g. M 1275 (1100–1500) n = 4 Panama, 1817 (1250–2150) n = 3 Argentina. F 1000 n = 1 Panama, 1500 n = 3 Argentina, 1560 n = 1 Tierra del Fuego. *P. b. mexicanus* Wing: M 271.4 (253–287) n = 7. F 253.4 (242–266) n = 8. Tail: M 159.2 (148–176) n = 4. F 150.6 (138–160) n = 8. Bill: M 46.6 (41–50) n = 7. F 45 (43–47) n = 8. Weight: M 1393 (1150–1550) n = 14. F 1256 (1100–1450) n = 8. Unspecified races (Telfair and Morrison 1995) Wing: M 263.4 (258–270) n = 10. F 245.9 (241–253) n = 10. Tail: M 159.8 (152–171) n = 10. F 145.8 (141–155) n = 10. Bill: M 48.0 (45–52) n = 10. F 46.0 (43–48) n = 10. Weight: M 1260 (n = 14). F 1070 (n = 70). Wing load 107 cm/g; aspect ratio 2.68; buoyancy index 4.8 (Hartman 1961).

Little black cormorant

Wing: M range of means 251–262 (various samples) extremes 229 and 280 mm New Zealand (skins) 251 (229–264) n = 4; NSW (live) 262 (250–280) n = 39. F range of means 240.1–246.3 (various samples) extremes 225–270 mm New Zealand (skins) 243 (230–259) n = 9; NSW (live) 245 (240–270) n = 31. Tail: M range of means 125.3–136; extremes 113–157. New Zealand (skins) 126 (121–128) n = 5; NSW (live)

136 (125–157) n = 34. F range of means 123–128.3 extremes 108 & 148. New Zealand (skins) 123 (108–141) n = 8; N.S.W. (live) 128 (113–148) n = 25. Bill: M range of means 46.7–48.5 extremes 41.7 & 53.0 New Zealand (skins) 48 (41–53) n = 5; N.S.W. (live) 48 (42–52) n = 38. Weights: M New Zealand (label data) 913 (517–1210); N.S.W. (live) 1100 (800–1300). F New Zealand (label data) 704.6 (576–865); N.S.W. (live) 900 (700–1,300) n = 34.

Great cormorant

P. c. carbo (various localities). Wing: M 357 (350–363) n = 6; F 339 (318–351) n = 12. Tail: M 154 (141–159) n = 6; F 150 (135–163) n = 12. Bill: M 69.6 (67–73) n = 6; F 63.7 (59–68) n = 12. Tarsus: M 74 (68–78) n = 6; F 70.6 (67–74) n = 12. *P. c. sinensis* (Netherlands) Wing: M 347 (330–364) n = 38; F 325 (311–337) n = 18. Tail: M 155 (145–165) n = 38; F 144 (133–154) n = 18. Bill: M 62.6 (58–67) n = 34; F 55.7 (50–58) n = 15. Tarsus: M 69.4 (66–73) n = 38; F 66.1 (64–70) n = 18. Kortlandt (*in litt*) says 5–10% females have larger bills than their mates. *P. c. lucidus* Wing: M 337.2 (322–353) n = 18; F 316.6 (300–332). Tail: M 139.8 (131–151) n = 16; F 132.0 (119–146) n = 10. Bill: M 68.6 (64–74) n = 17; F 61.6 (60–64) n = 15. *P. c. novaehollandiae* Wing: M 346 (332–355) n = 11; F 325 (312–338) n = 10. Tail: M 153 (149–165) n = 11; F: 144 (135–153) n = 10. Bill: M 70 (64–73) n = 11; F 62 (59–72) n = 10. Weights: *P. c. carbo* M: 3170, 3600; F 2127, 3490. *P. c. sinensis* M 2529 n = 55; F 2025 n = 25. *P. c. lucidus* M 3090 n = 3; F 1780 (1590–1930) n = 3; 2950 n = 2. *P. c. novaehollandiae* M 2508 (2253–2954) n = 6; F 1941 (1545–2110) n = 5.

Cape cormorant

Wing (unsexed): 254 (245–275) n = 10. Tail: 95 (86–100) n = 10. Bill: 54 (50–56) n = 10. Weight: M 1171 (800–1550); 1330 n = 24; 1306 large sample. F 1142 (1000–1225) n = 6; 1104 n = 11; 1155 large sample. Immatures (unsexed) 1160.

Socotra cormorant

Wing: M 285–310; 288; 296; 298.3 (285–303) n = 18. Juv 293.5 (274–304) n = 11. F 275–298; 281.9 (273–289) n = 10. Juv 279.2 (270–297) n = 11. Tail: M 85; 94.9 (90–102) n = 14. Juv 90.8 (72–103) n = 10. F 86.7 (82–92) n = 7. Juv 86.9 (80–95) n = 8. Bill: M 69; 73; 71.4 (64.2–76.5) n = 18. Juv 72.5 (66.0–77.7) n = 11. F 66.9 n = 10. Juv 69.9 (63.8–75.3) n = 10. Tarsus: M 73; 75; 75.5 (71.5–80.0) n = 18. Juv 74.7 (70.2–79.0) n = 10. F 71.4 (67.7–75.4) n = 10. Juv 72.7 (69.9–75.0) n = 12 (all measurements from freshly dead birds from Keijl and Symens 1993).

Bank cormorant

Wing: M 292 (277–309) n = 6. F 276 (262–291) n = 6. Tail: M 129 (113–137) n = 17. F 117 (107–132) n = 44. Bill: M 60.3 (56–64.5) n = 39. F 56.9 (50–62.5) n = 44. Tarsus: M 66.6 (62–70.5) n = 37. F 63.7 (61–66) n = 40. Weight: M 2107 (1775–2425) n = 77 (all paired); 1985 (max 2183) n = 21. F 1794 (1500–2150) n = 92 (all paired); 1700 (max 1958) n = 14.

All paired means a member of a pair

Japanese cormorant

Wing: M 330 (326–337) n = 6. F 315 (305–325) n = 11. Tail: M 140 (135–146) n = 6. F 135.7 (128–144) n = 8. Bill: M 70.1 (67.4–71.8) n = 6. F 63.9 (59.2–72.5) n = 12. Tarsus: M 70.5 (67–73) n = 6. F 65.8 (62–70) n = 12. Weight: M 3325. F 2394 (2356–2419) n = 3; 2860; 2460 (immature). Unsexed 2542; 2587.

Brandt's cormorant

Wing: M 290.3 (270–300) n = 17; 291 (274–305) n = 27. F 273.9 (262–293) n = 9; 270 (258–276). Bill: M 70.9 (67–77) n = 17. F 65.9 (63.5–69) n = 9. Weight: c2450 g.

European shag

P. a. aristotelis Wing: M 271 (261–278) n = 12. F 258 (251–269) n = 18. Tail: M 129 (119–133) n = 6. F 119 (114–125) n = 10. Bill: M 56.4 (51–61) n = 45. F 56.7 (51–63) n = 34. Tarsus: M 64.7 (62–68) n = 12. F 62 (58–65) n = 18. Weight: M 1919 g (1757–2284) n = 9 (range of individual trapped 4 times in a season, 200 g); breeding (Isle of May) 1360–2300 n = 303. F 1600 (1407–1788); breeding (Isle of May) 1395–1950 n = 250. *P. a. desmarestii* Wing: M 258 (243–271) n = 12. F 249 (240–265) n = 11. Bill: M 61 (58–65) n = 6. F 63 (61–65) n = 5. Vaurie (1965) gives male bill *desmarestii* as 69.2 n = 7; F 69.4 n = 9 compared with *aristotelis* M 59 n = 10; F 58.8 n = 10.

Pelagic cormorant

Wing: M 239–290 n = 24; *P. p. pelagicus* 276.5 n = 15; *P. p. resplendens* 255.3 n = 9. F 244–274 n = 16; *P. p. pelagicus* 260.7 n = 6; *P. p. resplendens* 252.3 n = 10. Tail: M & F c150–180. Bill: M 43–56; *P. p. pelagicus* 50.2 n = 15; *P. p. resplendens* 48.7 n = 9. F 44–50; *P. p. pelagicus* 47 n = 6; *P. p. resplendens* 47.2 n = 10. Weight: Adult M *P. p. pelagicus* 2034 (1814–2440) n = 9; Adult F 1702 (1474–2041) n = 5. Adults of both sub-species, M 2005 (1888–2097) n = 3; F 1523 (1214–1631) n = 5. See Hobson (1997) for more details.

Red-faced cormorant

Wing: M 277.3 (269–288) n = 6. F 272.2 (255–296) n = 9. Tail: M and F c180–200. Bill: M 53.8 (50–58) n = 6. F 55.5 (50–58.5) n = 9. Weight: M 2208 (1922–2267) n = 15, 2492, 2551. Immatures c2400 n = 3. F 1857 (1550–2050) n = 14, 1644, 1937.

Rock shag

Wing: M 252.2 (233–263) n = 15. F 244.7 (236–255) n = 29. Tail: M 138.6 (127–155) n = 15. F 133 (123–146) n = 29. Bill: M 52.7 (48.5–54.5) n = 15. F 51.0 (46–55) n = 29. Weight: M 1553 (1440–1680) n = 7. F 1445 (1360–1551) n = 4; 1417 (1300–1550) n = 10.

Guanay cormorant

Wing: M 296.4 (281–303) n = 5. F 281 (270–287) n = 4. Tail: M 100 (96–104) n = 5. F 103.3 (96.6–108.5) n = 4. Bill: M 71.4 (65–78) n = 5. F 69.1 (65–73) n = 4. Tarsus: M 68.8 (66–71) n = 5. F 66.6 (66–67). Weight: M 2832 (2478–3222) n = 3. Mean of unsexed adults (number unspecified) 1800 and 2072 ± 53.8 (Hutchinson 1950).

Pied cormorant

Wing: M 318 (287–356) n = 27. F 300 (277–353) n = 26. Tail: M 145 (128–170) n = 26. F 135 (106–162) n = 25. Bill: M 73 (64–80) n = 27. F 67 (59–79) n = 25. Tarsus: M 68 (63–74) n = 27. F 64 (60–69) n = 26. Weight: M 2196 (1814–2472) n = 60. F 1715 (1361–2062) n = 175.

Black-faced cormorant

Wing: M: 276 (267–290) n = 12, skins; 278 (266–291) n = 3, live. F 259 (250–266) n = 14, skins; 266 (259–277) n = 5, live. Tail: M 107 (92–125) n = 12, skins; 100 (92–109) n = 3, live. F 99 (91–115) n = 14, skins; 104 (92–111) n = 5, live. Bill: M 51.4 (47.7–55.4) n = 13, skins; 53 (48–55) n = 3, live. F 48.4 (43.7–53.5) n = 14, skins; 51 (46–56) n = 5, live. Tarsus: M 61.3 (52.9–67.3) n = 13, skins; 61 (59–63) n = 3, live. F 59.3 (54.9–62.2) n = 15, skins; 60 (59–62) n = 5, live. Weight: 1515 g (sex and age unspecified) n = 30.

King shag

Measurements: New Zealand skins. Wing: M 312 (306–323) n = 9. F 298 (284–307) n = 10. Tail: M 123 (111–132) n = 9. F 116 (109–129) n = 9. Bill: M 66 (63–68) n = 9. F 64 (62–69) n = 10. Tarsus: M 74 (72–77) n = 7. F 70 (68–74) n = 9. Weight: M usually heavier than F. Adult M 2655 n = 1. F 2500 n = 1.

Stewart shag

Wing: M 293 (278–310) n = 10; 287 (260–330) n = 6. F 287 (269–314) n = 22; 292 (277–311) n = 9. Tail: M 113 (105–123) n = 10; 126.5 (116–140) n = 4. F 112 (104–122) n = 21; 122 (109–142) n = 8. Bill: M 54 (49–59) n = 10; 57 (53–63) n = 6. F 53 (48–60) n = 22; 58 (51–69) n = 9. Tarsus: M 66 (62–70) n = 9; 59.5 (56–58) n = 6. F 65 (61–72) n = 18; 58.5 (55–64) n = 9. N.B. except for tarsus, all measurements in set 1 exceed those in set 2, presumably due to observer difference. Weight (label data): M 2717 (1797–3875) n = 6. F 1814 (1447–2356) n = 8. Live adults: 2800 (2500–3100) n = 8. Live juvs: 2400 (2100–2700).

Chatham shag

Skins. Wing: M 286 (278–292) n = 5. F 271 (261–284) n = 5. Tail: M: 116 (109–124) n = 4. F 108 (99–116) n = 5. Bill: M 53 (51–56) n = 5. F 53 (52–55) n = 4. Tarsus: M 65 (62–69) n = 5. F 64 (58–69) n = 5. Weight: label data M 5525 (fat); F 2230 (fat) and 1790.

Auckland shag

Wing: M 283 (265–291) n = 5; 269 (255–283) n = 12. F 268 (267–271) n = 4; 263 (237–278) n = 15. Tail: M 121 (116–127) n = 4; 117 (112–126) n = 12. F 110.5 (104–119) n = 4; 115 (103–126) n = 15. Bill: M 51 (49–56) n = 5; 51 (47–54) n = 10. F 48 (47–49) n = 3; 49 (45–53) n = 15. Tarsus: M 62 (58–64) n = 5; 63 (57–67) n = 12. F 60 (57–62) n = 4; 61 (59–65) n = 15. Weight: no details.

Campbell shag

Wing: M 282.5 (280–285) n = 2. F 272.5 (263–280) n = 8. Tail: M 117.5 (105–130) n = 2. F 119 (115–125) n = 8. Bill: M 53.5 (52–55) n = 2. F: 50 (47–52) n = 8. Tarsus: M 56.5 (55–58) n = 2. F 59 (55–62) n = 8. Weight: M 2041 g; 2097 g. F 1750 (1616–1927) n = 8.

Bounty shag

Skins. Wing: M 291.6 (285–300) n = 8; 294 (285–300) n = 11. F 279.5 (272–289) n = 7; 278 (272–287) n = 10. Tail M: 125.4 (117–133) n = 7; 127 (117–134) n = 11. F 115.3 (114–116) n = 3; 116 (107–137) n = 8. Bill: M 58.2 (56.2–60) n = 8; 59 (56–62) n = 11. Tarsus: M 67.7 (64.2–72) n = 8; 69.0 (67–71)

n = 10. F 65.9 (62.1–68.8) n = 8; 67.0 (65–70) n = 10. Weight: M 2500 (2300–2900) n = 7. F 2500 (2000–2700) n = 6.

Pitt shag

Wing: M 243 (228–255) n = 12. F 228 (209–243) n = 9. Tail: M 90 (81–97) n = 13. F 90 (75–103) n = 9. Bill: M 52 (48–54) n = 12. F 49 (44–51) n = 9. Tarsus: M 56 (52–61) n = 13. F 55 (52–58) n = 9. Weight: M 1325 n = 1. F 1078 and 1127.

Imperial shag

Wing: M 284 (282–287) n = 3. F 271.4 (258–282) n = 10. Tail: M 124 (117–131) n = 3. F 121.4 (117–131) n = 3. Bill: M 61.8 (59–64) n = 3. F 57.8 (55–60) n = 10. Weight: M 2721 (2104–3341) n = 5. F 2193 (2087–2389) n = 3.

Antarctic shag

Unsexed, presumed adults. Wing: 325 (320–330) n = 8. Bill: 59 (57–62.5) n = 8. Tail: 146 (136–158) n = 8. Weight: 2994 (2750–3250). Also M 3022 n = 16. F 2576 n = 21.

South georgian shag

Signy Island. Wing: M 304.5 n = 36. F 289.6 n = 23. Tail: M 137.0 n = 36. F 128.6 n = 24. Bill: M 48.4 (44–51) n = 5. F ?. Tarsus: M 62.5 (61–64) n = 4. F ?. Weight: M 2883 n = 130. F 2473 n = 101.

Heard shag

Skins. M Wing: 322 (305–335) n = 9. Tail: 129 (116–136) n = 9. Tarsus: 69 (65–70) n = 9. F: similar in all measurements, separate figures not available. Green (1997b) gives Wing: M 313 + 4 n = 3. F 289 + 3 n = 3. Bill: M 57.2 + 2. F 54.8 + 3. Tarsus and middle toe: M 90.4 ± 2. F 87.0 ± 2. Weight: M 3157 ± 64 n = 4. F 2467 ± 97 n = 3.

Crozet shag

Wing: M 286 (272–299) n = 8. F 268 (257–277) n = 8. Tail: M 131 (124–137) n = 4. F 112 (106–115) n = 3. Bill: M 58 (56–64) n = 8. F 56 (55–60) n = 8. Tarsus: M 62.9 (61–65) n = 8. F 57 (50–65) n = 8. Weight: M 2450 (1700–2700) n = 5. F 2040 (1950–2250) n = 5.

Kerguelen shag

Wing: M 272 (254–280) n = 9. F 263 (248–281) n = 11. Tail: M 107; 109. F 99; 102. Bill: M 50.3 (46–52) n = 9. F 47 (45–52.5) n = 11. Tarsus: M 58 (62–64) n = 9. F: 54.1 (50–60) n = 11. Weight: M 2000 (1840–2240) n = 3. F 1600 (1500–1730) n = 3. Unsexed adults 2630 (2100–3300) n = 27.

Macquarie shag (Brothers 1985)

Wing: M 309 (303–317) n = 8. F 293 (287–296) n = 8. Bill: M 59.5 (57.3–61.7) n = 8. F 54.8 (51.3–56.9) n = 8. Tarsus: M 66.3 (63.5–68.4) n = 8. F 63.5 (60.8–66.4) n = 8. Weight: M 3320 (2950–3500) n = 8

(before breeding season); 2864 (2650–3200) n = 16 after breeding season. F 2700 (2550–2990) n = 8 (before breeding season); 2434 (2180–2700) n = 18 (after breeding season). Sexes reliably recognized by measurements.

Red-legged cormorant

Wing: M 248 (240–254) n = 10 Peru and Chile. F 239 (232–245). Tail: M 97.0 (92–101). F 97.5 (92–103). Bill: M 58.2 (55–62) n = 10. F 58.8 (55.5–62) n = 8. Tarsus: M 52.2 (50–54) n = 10. F 51.4 (50–54) n = 8. Weight (sex not specified): 1304–1417. M 1471 (1375–1550) n = 6. F 1433 (1400–1500) n = 3.

Spotted shag

P. p. punctatus Wing: M 248 (235–264) n = 17. F 244 (233–266) n = 29. Tail: M 87 (70–97) n = 17; 85 (78–79) n = 29. Bill: M 61 (56–70) n = 17; 60 (56–61) n = 29.

P. p. oliveri Wing: M 251 (238–272) n = 8. F 243 (231–255) n = 8. Tail: M 86 (79–102) n = 8. F 83 (77–92) n = 8. Bill: M 59 (54–64) n = 8. F 57 (54–61) n = 8. Weight: M 1210 (850–1670) n = 14. F 1160 (770–1610) n = 8.

Little pied cormorant

P. m. melanoleucos Wing: M 234.6 (226–244) n = 22; 235 (219–246) n = 14. F 228.8 (215–242) n = 26; 227 (215–238) n = 19. Tail: M 151.2 (141–167); 163 (150–178) n = 4. F 149.4 (140–167) n = 27; 152 (145–165) n = 11. Bill: M 30.2 (28.3–33.0) n = 22; 32.0 (29–36) n = 11. F 30.4 (26–34.4) n = 27; 31 (26–33) n = 21. Tarsus: M 38.6 (34.3–40.9) n = 19; 40 (36–42) n = 12. F 37.8 (33–39.9) n = 21; 40 (37–50) n = 15. Weight (fresh N.S.W.): M 800 (700–900) n = 17. F 700 (400–900) n = 30.

P. m. brevirostris Wing: M 232 (221–246) n = 13. F 225 (214–239) n = 28. Tail: M 150 (131–164) n = 13. F 145 (133–153) n = 28. Bill: M 30 (26–33) n = 13. F 30 (27–33) n = 28. Tarsus: M 40 (35–42) n = 13. F 39 (36–45) n = 26.

Long-tailed cormorant

P. a. africanus Wing: M 215 (205–224) n = 10; 212 (206–219) n = 6. F 209 (196–221) n = 9; 207 (194–216) n = 8. Tail: M 158.6 (147–174) n = 10; 149 (144–153) n = 5. F 152.9 (143–160) n = 8; 148 (139–164) n = 5. Bill: M 30.4 (28–31) n = 13; 30.7 (29–33) n = 6. F 29.0 (no range) n = 9; 30.4 (26–32) n = 8. Tarsus: M 38.6 (36–41) n = 14. F 37.9 (34–40) n = 9. Weight: M 568.5 n = 40; 544 (505–635) n = 12. F 513 n = 10; 546.0 (435–600) n = 7. *P. a. pictilis* slightly larger with longer wings.

Crowned cormorant

Wing: M 213.9 (206–220) n = 10. F 207 (203–213) n = 6. Tail: M 131.7 (123–141) n = 7. F 138.3 (136–142) n = 3. Bill: M 29.6 (28–31) n = 10. F 28.4 n = 8. Tarsus: M 46.6 (42–52) n = 11. F 45.1 (41–49) n = 8. Weight: M 675 (475–775) n = 4; 797.7 (710–880) n = 6; 756 n = 5. F 730 (700–775) n = 5; 728 (670–780) n = 5.

Javanese cormorant

Wing: M 196 (190–200) n = 4. F 194 (185–200) n = 4. Tail: M 134.5 (130–139) n = 4. F 126 (117–130) n = 4. Bill: M 29.7 (28–32) n = 4. F 29.5 (28–30) n = 4. Weight sex and sample unspecified: 427 g (360–525).

Pygmy cormorant

Wing: M 206 (195–217) n = 11. F 201 (193–208) n = 7. Tail: M 142 (137–145) n = 6. F 141 (137–147) n = 5. Bill: M 30.5 (29–33) n = 6. F 29.2 (27–31) n = 5. Tarsus: M 38 (37–40) n = 6. F 37.8 (36–39) n = 5. Weight: M 650, 710, 870. F 564, 640, 640.

Flightless cormorant

Wing: M 186–188. F 177.5–193. Tail: M 154–165. F 149–165. Bill: M 65–77. F 59–76. Tarsus: M 72–79. F 59–66. Weight: M 3958 (3800–4090) n = 4. F 2715 (2500–2900) n = 4. Tindle (1984) claims evidence for dis-assortative mating, the heavier the male and the lighter and more slender-billed his mate but statistics significant only at 0.05 level of probability.

Anhinga and darter

Anhinga

Wing: M (316–347) n = 58. F (312–361) n = 44. Bill: M (74–98.8) n = 58. F (74–91.5) n = 44. Weight: M 1262 n = 15, Unsexed 1254 n = 54, F 1215 n = 13

Darter

Wing: *A. m. rufa* M 349 (328–364) n = 8, F 344 (331–360) n = 7. *A. m. melanogaster* (unsexed) 331–357. *A. m. novaehollandiae* M 351 (329–373) n = 11, F 344 (304–375) n = 26.

Tail: *rufa* M 238 (229–253) n = 8, F 239 (233–248) n = 4. *melanogaster* (unsexed) 202–240. *novaehollandiae* M 215 (183–240) n = 46, F 215 (177–238) n = 25

Bill: *rufa* M 81 (75–89) n = 12, F 76 (71–78) n = 6, *melanogaster* (unsexed) (74–90). *Novaehollandiae* M 74 (61–81) n = 45, F 73 (54–85) n = 26.

Tarsus: *melanogaster* (unsexed) 42–47.

Weight: *rufa* M 1485 n = 11, 1292 (948–1815) n = 7, 1436 (1206–1711) n = 10, 1375 (1100–1600) n = 4, F 1530 n = 10, 1444 (1358, 1530) n = 2, 1298 (1150–1400) n = 6. *melanogaster* (unsexed) 1340 (1160–1500) n = 4, *novaehollandiae* M 1759 (1420–2100) n = 9, 1600 (1200–2100) n = 16, F 1790 (1300–2077) n = 9, 1700 (900–2600) n = 18.

Frigatebirds

Ascension frigatebird

Wing skins: M 562 (552–581) n = 5. F 598 (587–607) n = 4. Tail: M 384 (357–402) n = 5. F 405 (393–411) n = 4. Bill: M 91.7 (87.3–95.5), n = 5. F 103 (99–105.9) n = 4. However, Stonehouse gives culmen length of chicks 121–140 days as 120 mm—significantly larger than either of adult measurements given above. Tarsus (unsexed): 57 n = 5 (this figure from Murphy (1936) but seems suspect). Weight (unsexed): 1247 g n = 5.

Christmas frigatebird

Wing: M 610 n = 10; 616; F: 650 n = 10; 648; skin 634. Tail: M 388 n = 10; 418; 386; skin 355. F 419 n = 10; 468; 411; skin 436. Bill: M 131 (to gape) n = 10; 110.5; skin 103.1. F: 157 (to gape) n = 10; 131.8; skin 136.8. Tarsus: M skin 25. F skin 18.9. Weight: M 1400. F 1550.

Magnificent frigatebird

Wing: M 633 (611–661) n = 21 various localities excluding Galapagos; 653 (630–680) n = 9 Galapagos. F 650 (628–674) n = 21 various excluding Galapagos; 710 (695–735) n = 10 Galapagos. Wing area: M 3610 sq cm. F 3725 sq cm. Tail: M 431 (339–472) n = 21. F 431 (404–506) n = 21 (NB Murphy (1936) cited his range incorrectly, so av probably incorrect too). Bill: M 112.1 (105.2–118.5) excluding Galapagos; 106 (101–113) Galapagos (NB seems fishy that Galapagos M should have smaller bills than non-Galapagos but bigger wings, whilst Galapagos F has bigger bills than other females as one would expect). F 121 (109.2–130) excluding Galapagos; 128 (124–132) n = 10 Galapagos. Tarsus: M 22.4 (21–25). F 22.9 (21–25). Weight: M 1401 (1310–1525) n = 5. F 1587, 1633 (1500–1840) n = 5. Wing loading (g/sq cm): M 0.3890. F 0.4391. Calculated by planimeter from specimens, Harrison *et al.* (1972).

Great frigatebird

Wing: M 562.4 (552–570) n = 5 Christmas Island (IO); 581.6 (540–612) n = 12 Cocos Keeling; 608 Aldabra; 582 Coral Sea. F: 587 (582–592) n = 3 Christmas Island (IO) 606.9 (552–638) n = 13 Cocos Keeling; 610 Aldabra; 607 Coral Sea. Tail: M 378.5 (370–390) n = 4 Christmas Island (IO); 390.5 (314–428) n = 12 Cocos Keeling; 427 Aldabra; 397 Coral Sea. F: 402.3 (385–415) n = 3 Christmas Island (IO); 414.5 (392–444) n = 13 Cocos Keeling; 386 Aldabra; 415 Coral Sea. Bill: M 95.6 (92–98) n = 5 Christmas Island (IO); 102 (96–108) n = 12 Cocos Keeling; 99.5 and 96 (92–100) n = 13 Galapagos; 104 Aldabra; 102 Coral Sea. F: 106.7 (105–108) n = 4 Christmas Island (IO); 115.9 (105.5–123) n = 13 Cocos Keeling; 112.5 and 111 (106–121) n = 24 Galapagos; 117 Aldabra; 116 Coral Sea. Tarsus: M 26.7 (25–28) n = 12 Cocos Keeling; F: 28.3 (26–30) n = 13 Cocos Keeling. Weight: M 1239 (950–1450) Galapagos; 1201 (1000–1450) n = 21 Aldabra; 1075 and 1150 Christmas Island (IO). F: 1630 (1400–1950) Galapagos; 1427 (1215–1640) n = 21 Aldabra.

Lesser frigatebird

Wing: M 533.5 (518–550) n = 4 Cocos Keeling; 538 (mean) Aldabra; 534 (mean) Coral Sea; 508–554 Malaya. F 547 (534–562) n = 5 Cocos Keeling; 560 (551–556) n = 4 Queensland; 553 (mean) Aldabra; 547 (mean) Coral Sea; 526–580 Malaya. Tail: M 316.5 (307–331) n = 4 Cocos Keeling; 325 (mean) Aldabra; 317 (mean) Coral Sea. F 356.2 (347–364) n = 4 Queensland; 318.4 (314–324) n = 5 Cocos Keeling; 324 (mean) Aldabra; 318 (mean) Coral Sea. Bill: M 82.2 (79–85) n = 4 Cocos Keeling; 80 (mean) Aldabra; 83 (mean) Coral Sea; 81–91 Malaya. F 89.4 (86–93) n = 5 Cocos Keeling; 90.1 (87.5–91.9) n = 4 Queensland; 87 (mean) Aldabra; 88 (mean) Coral Sea; 88–95 Malaya. Tarsus: M 22.7 (22–23.5) n = 4 Cocos Keeling. F 24.9 (24–25.5) n = 5 Queensland. Weight: M 754 (625–875) n = 29 Aldabra. F 942.2 (780–1107) n = 4 Queensland; 970; 1246; 858 (760–955) n = 45 Aldabra.

Tropicbirds

Red-billed tropicbird (skins)

Wing: M 310 (296–330) n = 9. F 313 (307–319) n = 6.
Tail (– streamer): M 114(109–120) n = 7. F 110 (105–120) n = 5.
Bill: M 62.1 (59–65) n = 10. F 61.4 (60–66) n = 7.
Tarsus: M 29.5 (28–31) n = 10. F 28.1 (27–29) n = 7.
Weight: (live and unsexed) Ascension 750 g S Plaza, Galapagos 642.

Red-tailed tropicbird

Males slightly larger than females but too much overlap to allow reliable sexing.

Wing (skins): M 345 (338–353) n = 5. F 338.4 (320–356) n = 5. Unsexed live 353 (335–375) n = 30; 335.9 (338–353) n = 20. Tail (skins excluding streamers): M 107.6 (96–112) n = 5. F 107.2 (100–117) n = 5. Tail (including streamers): M 395.8 (280–457) n = 5. F 404 (380–443) n = 5. Tarsus (unsexed): 29.0 n = 13. Bill (skins): M 66.9 (65–70) n = 5. F 65.9 (63–69) n = 5. Live unsexed 67 (61.8–70.5) n = 30. Weight unsexed: 774.2 (590–1095) n = 38. Comparing measurements at extremes of cline, i.e. Norfolk Island and Kure Atoll: Norfolk wing: 348.9 ± 1.8 . Bill: 66.4 ± 0.4 . Kure wing: 319.2 ± 1.0 . Bill: 62.4 ± 0.3 .

White-tailed tropicbird

Wing: M 276.3 (273–281) n = 6; skins 277.3 (272–282) n = 3; 263.8 (260–270) n = 5. F skins 269 (267.5–271.5) n = 3; 263. Tail (including streamers): M 413 (355–501) n = 7; 362.6 (318–427) n = 3; 386.5 (346–455.5) n = 5. F 440.5 (426.5–452) n = 3. Tail (excluding streamers): M 107.6 (96–130) n = 3. F 91.0. Bill: M 49.4 (48–51) n = 7; 50.0 (49.5–51.1) n = 3; 47.4 (45–50.7) n = 5. F 43.5; 46.3 (45.5–47.1) n = 3. Unsexed 49.0 n = 59. Tarsus: M 23.5 (23–25) n = 7; 21.3 (19–23.3) n = 3; 21.4 (20.8–22.4) n = 5. F 22.5; 20.3 (20.1–20.5) n = 3. Unsexed 22.0 n = 36. Weight label data: M 295 (220–345) n = 3; 262.4 (230–275) n = 5. F 220.0; 305 (290–335) n = 3. Unsexed ads 330 (230–410); 321 (280–365) n = 6. Specific areas: Seychelles live, unsexed 334 n = 59. Unsexed Bermuda 407. Ascension 300. Christmas Island (IO) grounded and therefore some underweight, unsexed ads wing: 281 (270–295) n = 14. Tail excluding streamers: 113 (85–130) n = 14; longest streamer: 425 (315–540) n = 14. Bill: 48.7 (45.8–51.4) n = 14. Weight: 291.6 (245–376) n = 14. The following unsexed measurements of skins from Corre and Jouventin (personal communication) show size differences between sub-species. *P. l. lepturus* wing: 274 ± 6 ; bill: 48.9 ± 2.7 ; tarsus 220 ± 1.3 n = 34. *P. l. fulvus* wing: 280 ± 5 ; bill: 49.6 ± 1.2 ; tarsus: 21.9 ± 0.8 . n = 12. *P. l. dorotheae* wing 265 ± 7 ; bill 46.5 ± 2.1 ; tarsus 19.6 ± 0.9 n = 8. *P. l. catesbyi* wing: 277 ± 7 ; bill: 51.7 ± 2.1 ; tarsus: 22.4 ± 0.8 n = 21. *P. l. ascensionis* wing: 264 ± 8 ; bill: 46.8 ± 3.3 ; tarsus 21.3 ± 1.1 n = 17. The Europa population wing: 261 ± 6 ; bill: 44.5 ± 1.7 ; tarsus: 21.6 ± 0.8 .

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Selective Glossary

Adaptive: conferring survival value

Advertising: for this book a ritualized display by which a male attracts a female to close quarters

Agonistic: behaviour motivated by a mixture of fear and aggression

Alar: the tract of feathers running across the wing, as in the 'alar bar' in juvenile frigatebirds

Allele (allelomorphs): alternative forms of the same gene. Each parent contributes one. An allele may be dominant, in which case it dictates the physical expression (phenotype) of the character (e.g. plumage type) where there are two or more alternatives

Altricial: helpless when hatched; often used of hatchlings (mainly naked) that remain in the nest

Appendicular skeleton: pectoral and pelvic girdle and limbs

Asymptotic: where a curved graph flattens out

Carotenoid: orange-red pigment

Cladistic (clades): a formulation of relationships based on degree of ancestral sharedness

Cooperative breeding: where three or more individuals (not necessarily related) cooperate in breeding, as, for example, in some Antarctic skuas. Not known in pelecaniforms

Crèche: an aggregation of pre-fledged birds, often in close contact

Cytochrome: a pigment containing iron and protein which is involved in respiration in living cells

Dimorphic: present in two colour-forms (not transitory phases) e.g. the brown form and white form of the red-footed booby

Displacement activity: an apparently irrelevant act often occurring when two incompatible motivational systems ('drives'), such as fleeing and attacking, are aroused simultaneously. In such a case the bird may perform, for example, displacement preening

DNA-DNA hybridization: a technique for measuring the degree of relationship between two species by 'melting' and reassembling their DNA molecules

Emarginated: when the distal part of the inner or outer web of a feather, usually a primary, is partly cut away (barbs indented)

Emigration: usually means moving away from the colony of birth to breed

Endemic: restricted to a particular locality, usually an island or group of islands

Eruption: a mass movement away from the usual area of residence, often after a catastrophic decline in food

Furcula: 'wish bone'—formed by fusion of right and left clavicles ('collar bones'); variably rigid in birds according to nature of flight

Genotype: the sum of the active genes

Hallux: the first toe, usually directed backwards and often reduced in size

Homologous: two or more structures or behaviours are homologous if they share a common

origin. The bird and bat wing are homologous, as are the several forms of sexual advertising displays in boobies

Incomplete regurgitation: adult regurgitates food into its throat, to be taken by chick, which inserts its bill/head. Common to all peleciforms except tropicbirds

Key stimulus: a feature (in birds usually visual or auditory) which has strong potential to release a response, usually from a conspecific—e.g. the red spot on the yellow beak of the adult herring gull which releases the pecking response of the hatchling

Kleptoparasitism: stealing food from other individuals—usually of a different species, e.g. in skuas robbing gannets

Leucistic: abnormal plumages due to partial loss of single pigments. Usually leucistic individuals are paler. ‘Albinism’ (complete loss of pigment) is commoner

Monophyletic: single evolutionary ancestry, contra polyphyletic

Morphology: the shape and structure of the body

Nares: external openings (nostrils) on the bill. Closed (occluded) in, for example, sulids

Neossoptile: the downy plumage with which some birds hatch

Nidicolous: hatchlings that remain in the nest; usually semi-naked and helpless, as in all peleciforms except tropicbirds

Occipital: the back of the skull (occiput)

Opportunistic (of breeding): breeding outwith a fixed seasonal regime in response to temporarily favourable conditions

Palaeartic: a zoogeographical region comprising much of Eurasia and Africa north of the Sahara

Pelagic: foraging far offshore

Phenotype: the outward (morphological) manifestation of the underlying genotype

Philopatry: returning to the same locality for successive breeding attempts (in natal philopatry the locality of birth)

Phylogeny: a taxonomic term indicating evolutionary history, of the taxon, contra ontogeny which is the development of the individual

Pod: see ‘crèche’

Polyparous: laying clutch of more than one egg

Precocial: can move around immediately after hatching

Rami: the two halves of the lower mandible (jaw bone), fused at the tip but joined by soft tissue at the base

Rectrices: main tail feathers

Remiges: main flight feathers (singular remex); primary or secondary wing feathers

Ritualized: behaviour which is stereotyped and (often) exaggerated and repetitive; used, for example, in courtship, chick-begging

Salt glands: function in excreting excess salt which seabirds (especially) ingest, but present in all birds. Consists of two or more lobes lying in depressions in the skull above or in front of the eye socket

Superspecies: where taxa are too closely related to merit full specific status but are more than mere sub-species, e.g. the three gannets

Synsacrum: the fused bones of the pelvic girdle

Taxonomy: the science of classification (Systematics) using a variety of features

Totipalmate: a bird’s foot with webbing between all four toes

‘Ultimate’: evolutionary causes or forces selecting for a characteristic—such as range of clutch size. Contrast ‘proximate’—short-term factors, such as food shortage, which may affect clutch size in a particular year

Uniparous: laying single-egg clutch

Index

The index is intended to be a reasonable guide rather than a detailed one, and, together with the contents list and the consistent format within the species accounts, should prove adequate. It does not include authors' names or geographical locations. Species accounts may be found on the page numbers set in **bold** type. Plates appear between pages 238 and 239.

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